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**THE LIFE HISTORY, BEHAVIOR AND CONSERVATION OF THE TIGER
SPIKETAIL DRAGONFLY (*CORDULEGASTER ERRONEA* HAGEN)
IN NEW JERSEY**

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ABSTRACT OF THE DISSERTATION

THE LIFE HISTORY, BEHAVIOR AND CONSERVATION

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This dissertation explores the life history and behavior of the Tiger Spiketail dragonfly (*Cordulegaster erronea* Hagen) and provides recommendations for the conservation of the species. Like most species in the genus *Cordulegaster* and the family Cordulegastridae, the Tiger Spiketail is geographically restricted, patchily distributed with its range, and a habitat specialist in habitats susceptible to disturbance. Most Cordulegastridae species are also of conservation concern and the Tiger Spiketail is no exception. However, many aspects of the life history of the Tiger Spiketail and many other Cordulegastridae are poorly understood, complicating conservation strategies.

In this dissertation, I report the results of my research on the Tiger Spiketail in New Jersey. The research to investigate life history and behavior included: larval and exuvial sampling; radio-telemetry studies; marking-resighting studies; habitat analyses; observations of ovipositing females and patrolling males, and the presentation of models and insects to patrolling males. The research reports: the first use of radio-telemetry for the species; the first observations of mating; the first comprehensive report and analysis of larval site emergence site selection; the triggering

mechanisms for male recognition of females; adult and larval habitat use, and many other life history and behavioral aspects of the species. The dissertation also provides recommendations for conservation strategies that maybe useful for protecting the Tiger Spiketail and other Cordulegastridae species.

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Chapter 1

The Life History, Behavior and Conservation of the Tiger Spiketail dragonfly

(*Cordulegaster erronea* Hagen) in New Jersey

INTRODUCTION TO THE DISSERTATION

Overview

Dragonflies are model organisms for ecological and behavioral studies (Corbet 1999, Cordoba-Aguilar 2010). They are ancient insects with a lineage dating back to the Carboniferous Period more than 300 million years ago (Grimaldi and Engel 2005). Dragonflies possess a vast range of behavioral characteristics occupying virtually every aquatic environment except the oceans, on every continent, except Antarctica. Their primitive origins and ecological and behavioral diversity are well suited to investigate a broad suite of insect evolution and ecology including mating behavior and territoriality (Suhonen *et al.* 2010). Dragonflies are also a bridge between aquatic and terrestrial environments and many species may be declining. Therefore, they should be an important component of habitat conservation priorities.

There is a vast body of literature on the Odonata dating back hundreds of years. Many of the studies have been conducted on territorial species, but with considerably fewer focused on non-territorial species like the Spiketails (Cordulegastridae), probably owing to the difficulty of tracking individual males and the typical infrequency of females at the mating place (Fincke *et al.* 1997). However, understanding the behavior of non-territorial species is important to answer questions regarding the evolution of many behaviors in Odonata (Corbet 1999). The non-territorial Cordulegastridae may be particularly suitable

for these studies as they retain many primitive characteristics and are basal to the higher Libellulidae (Carle *et al.* 2015, Fraser 1929, Fraser 1933, Ware *et al.* 2007, Ware *et al.* 2008) (Figure 1). Most *Cordulegaster* species also occupy habitats that are thought to be used by the most ancient dragonfly families (Corser *et al.* 2014). Therefore, they may help shed light on the evolution of mating behaviors and territoriality in Odonata (Fincke *et al.* 1997, Hančíková 2014, Kaiser 1982). This dissertation presents the findings of research on the Tiger Spiketail dragonfly (*Cordulegaster erronea* Hagen) including adult and larval behavior, habitat, and the implications for conservation. Radio-telemetry, larval sampling, exuvial sampling, wing marking, passive observations and GIS analysis were used to investigate the life history and behavior of the Tiger Spiketail.

STUDY ORGANISM

The Cordulegastridae or Spiketails are a small but almost cosmopolitan family of dragonflies (Needham *et al.* 2000). The female has a spike-like ovipositor that is unique to the family (Figure 2). The common name of “Spiketails” is derived from this ovipositor. Oviposition is in a nearly vertical posture with the eggs thrust into the substrate in an up and down movement. There are currently about 45 species in three genera with a Holarctic distribution (Garrison, *et al.* 2006). The genus *Cordulegaster* (Leach) has 24 known species all limited to the Northern Hemisphere, 14 in the Old World and 10 in North America (Garrison, *et al.* 2006, Needham *et al.* 2000) (Figure 3). Most *Cordulegaster* species have limited geographic ranges and are patchily distributed within habitats that are likely highly sensitive to disturbance (Corser *et al.* 2014, White *et al.* 2014). Many are also of conservation concern (IUCN 2015, NatureServe 2015). However, comprehensive life-histories for most *Cordulegaster* species are lacking,

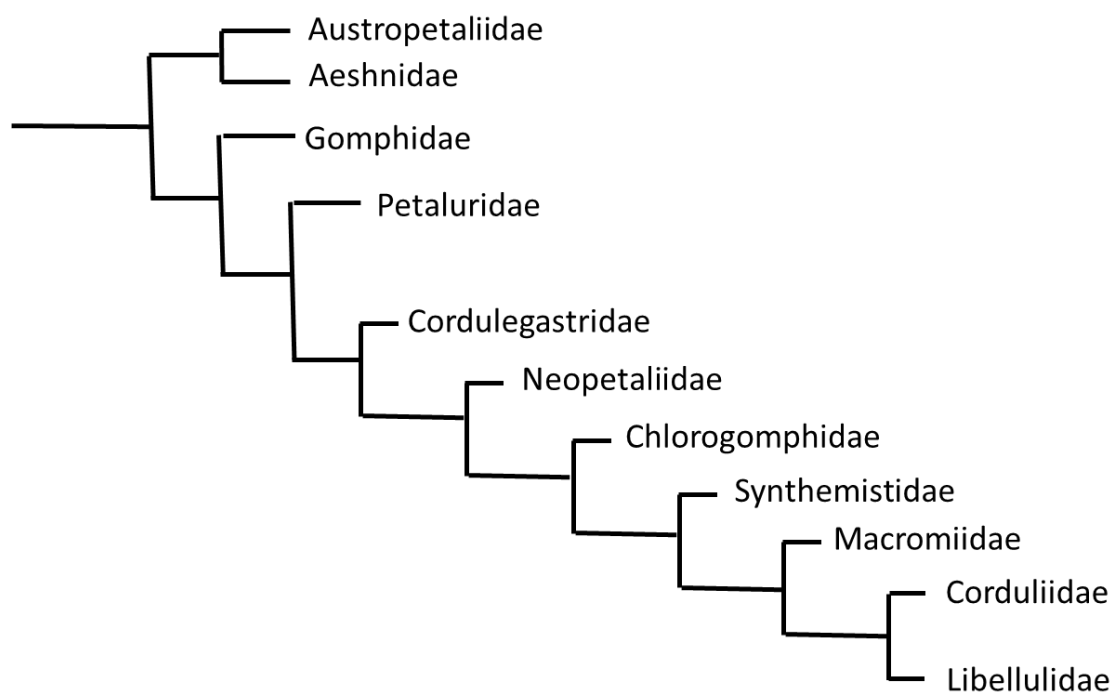


Figure 1. Current phylogenetic position of Cordulegasteridae. (After Carle *et al.* 2015)

potentially complicating conservation strategies.

The Tiger Spiketail is a large attractive dragonfly with bright green eyes and a black body with yellow stripes (Figure 4). There are only two previous *C. erronea* studies, one in New Jersey (Barlow 1995) and the other in Ohio (Glotzhober 2006). Only the Ohio study was extensive. *C. erronea* is listed as Threatened, Endangered, Critically Impaired, Special Concern, or of Greatest Conservation Concern in many states throughout its range (NatureServe 2015) (Table 1 and Figure 5). *C. erronea* is also patchily distributed (Figure 6). In New Jersey, the Tiger Spiketail is listed as a Species of Special Concern by the New Jersey Endangered & Nongame Species Program (ENSP) and has been assigned a New Jersey Natural Heritage State Rank of S2 - Imperiled. “Imperiled” is defined as “rarity due to very restricted range, very few populations (often 20 or fewer), steep declines, or other factors making it very vulnerable to extirpation from the nation or state/province.” (NatureServe 2015).

Predictive habitat models have been developed for *C. erronea* by the New Jersey Department of Environmental Protection (NJDEP) (NJDFW 2012) and the New York State Department of Conservation (NYNHP 2012) but are limited in their utility by the lack of detailed life history information. Without a better understanding of the larval and adult habitat characteristics, developing appropriate conservation strategies is hindered.

To assist in habitat protection measures for the species, *C. erronea* was recently added to the New Jersey Landscape Project mapping, a species-based mapping model that identifies habitats for rare species throughout the state (NJDFW 2012). This mapping utility is utilized by the NJDEP and other regulatory agencies for various land use,



Figure 2. Female *Cordulegaster erronea*. (Top) – Female showing color pattern typical of the Corduleagstridae. (Bottom) – Close-up of the spike-like ovipositor that the common name “Spiketail” is derived from.

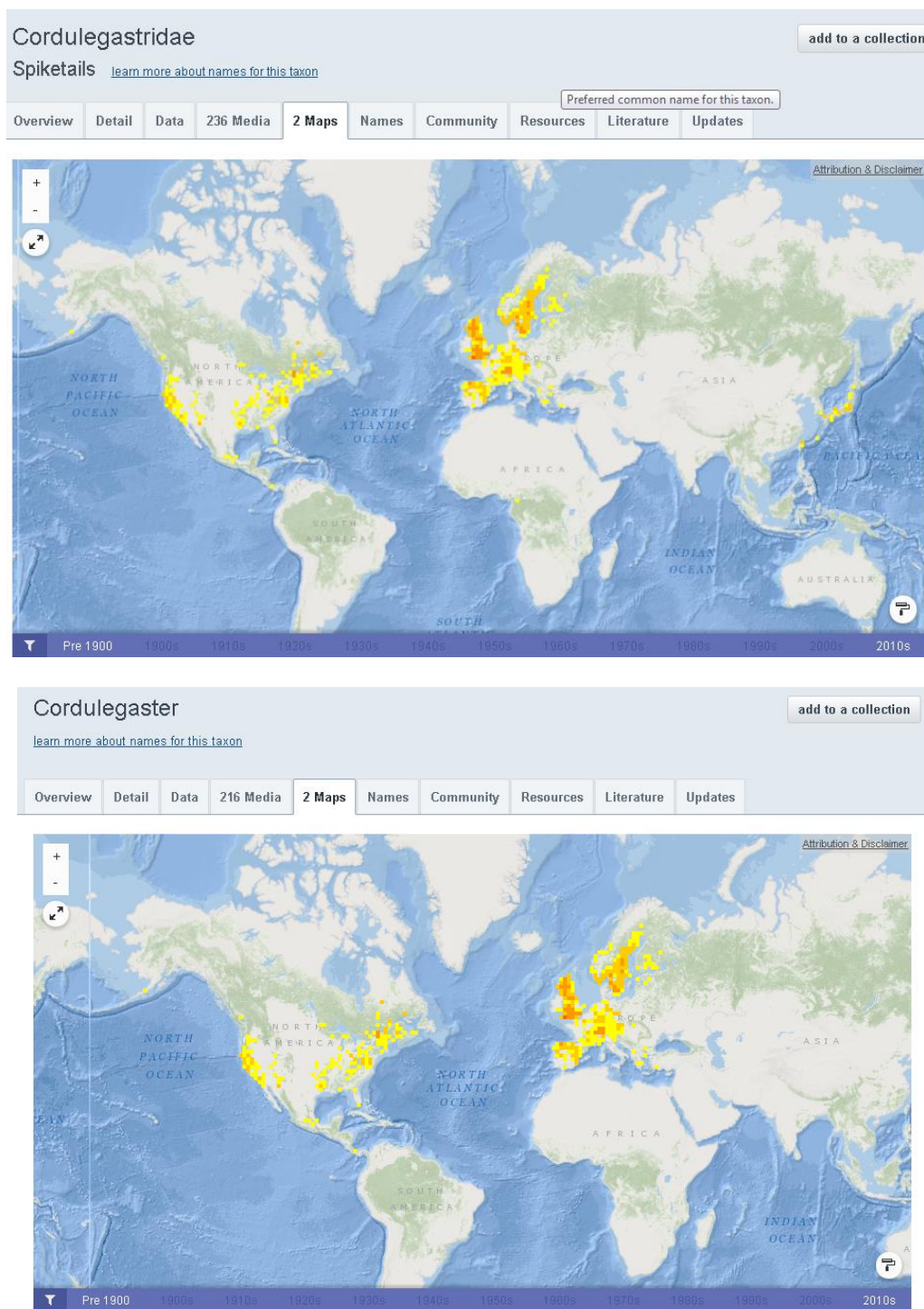


Figure 3. *Cordulegastridae* and *Cordulegaster* distribution. (Top) – Distribution of *Cordulegastridae*. (Bottom) – Distribution of *Cordulegaster*. Source: Encyclopedia of Life, available from <http://eol.org/pages/5251/maps>. Accessed 27 October 2015.



Figure 4. Female (left) and male (right) *Cordulegaster erronea*.

Table 1. Conservation status of *Cordulegaster erronea*

State	State Listing	NHP State Ranking	Source
New Jersey	Species of Special Concern	S2	NJDEP 2012
Connecticut	Threatened	S1	CTDEEP 2015
New York	Not Listed	S1	NYNHP 2013
Ontario	Not Listed	S1	OMNR 2015
Indiana	Endangered	S1	IDNR 2013
Illinois	Not Listed	S1	NS 2015
Mississippi	Special Animals Tracking List	S1	MNHP 2015
Michigan	Special Concern (Rare or Uncertain)	S1/S2	MDNR 1999
Delaware	Species of Greatest Conservation Need	S2	DDFW 2006
Ohio	Threatened	S2	ODW 2015
West Virginia	R, T and Endangered Animals	S2	WVNHP 2012
Kentucky	Not Listed	S2	NS 2015
Maryland	Greatest Conservation Concern	S3	MDNR 2005
Virginia	Watch List	S3	Roble 2013
North Carolina	Not Listed	S3	NCNHP 2012
Georgia	Not Listed	S3	GDNR 2009
Pennsylvania	Not Listed	S3	PNHP 2015
Tennessee	Not Listed	S4	TDEC 2015
Alabama	Not Listed	NR/UR	ANHP 2014
Louisiana	Not Listed	NR/UR	NS 2015

Explanation of Natural Heritage Program State Ranking codes:

S1 - Critically Imperiled - Critically imperiled because of extreme rarity or because of some factor(s) making it especially vulnerable to extirpation or extinction. Typically 5 or fewer occurrences or less than 1000 remaining individuals.

S2 - Imperiled - Imperiled because of rarity or because of some factor(s) making it very vulnerable to extirpation or extinction. Typically 6 to 20 occurrences or between 1,000 and 3,000 remaining individuals.

S3 - Vulnerable - Vulnerable either because rare and uncommon, or found only in a restricted range (even if abundant at some locations), or because of other factors making it vulnerable to extirpation or extinction. Typically 21 to 100 occurrences or between 3,000 and 10,000 remaining individuals.

S4 - Apparently Secure - Uncommon but not rare, and usually widespread. Possible cause of long-term concern. Usually more than 100 occurrences and more than 10,000 individuals.

NR/UR – Not Ranked/Under Review - Rank not yet assessed.

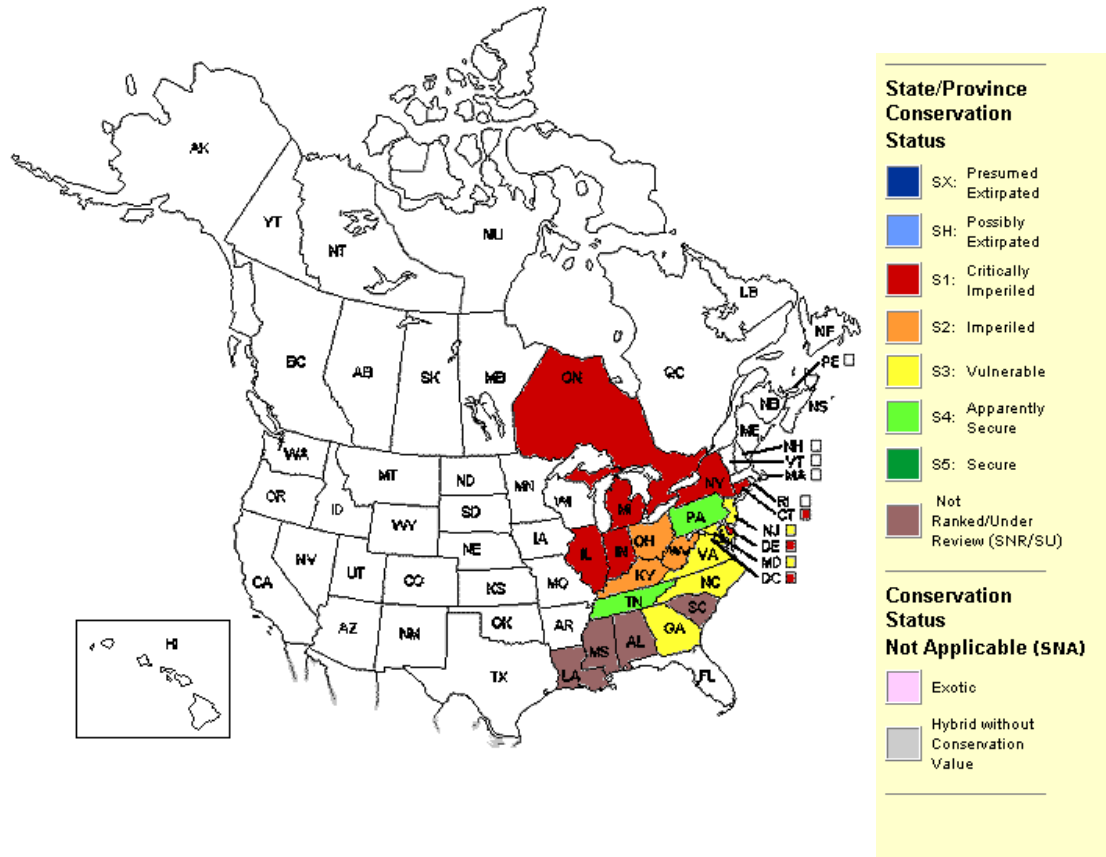


Figure 5. Rangewide conservation status of *Cordulegaster erronea*. Source: NatureServe. 2015. NatureServe Explorer: An online encyclopedia of life [web application]. Version 7.1. NatureServe, Arlington, Virginia. Available <http://explorer.natureserve.org>. (Accessed: October 23, 2015).

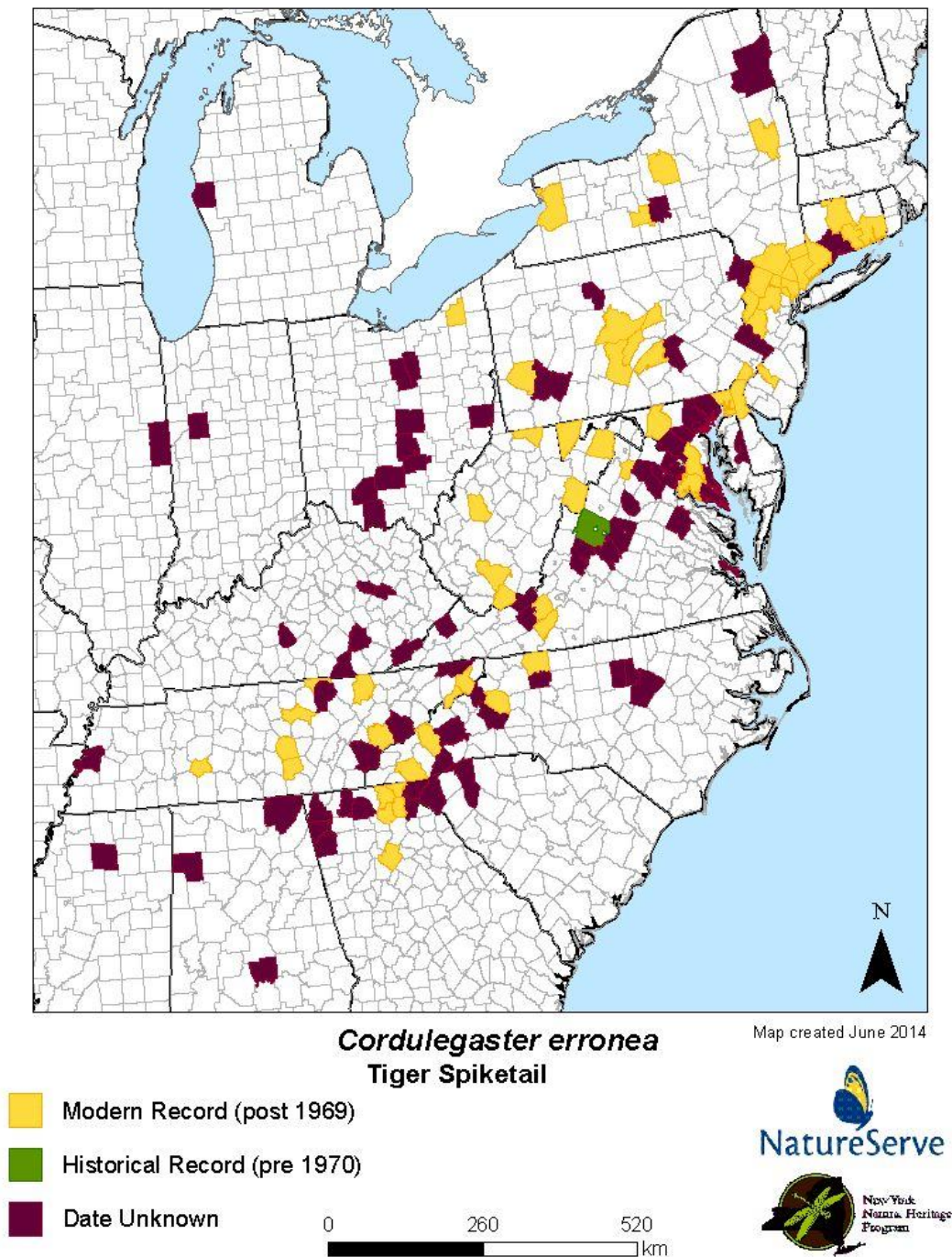


Figure 6. Distribution of *Cordulegaster erronea* by county. Source: NatureServe. 2015. NatureServe Explorer: An online encyclopedia of life [web application]. Version 7.1. NatureServe, Arlington, Virginia. Available <http://explorer.natureserve.org>. (Accessed: November 9, 2015).

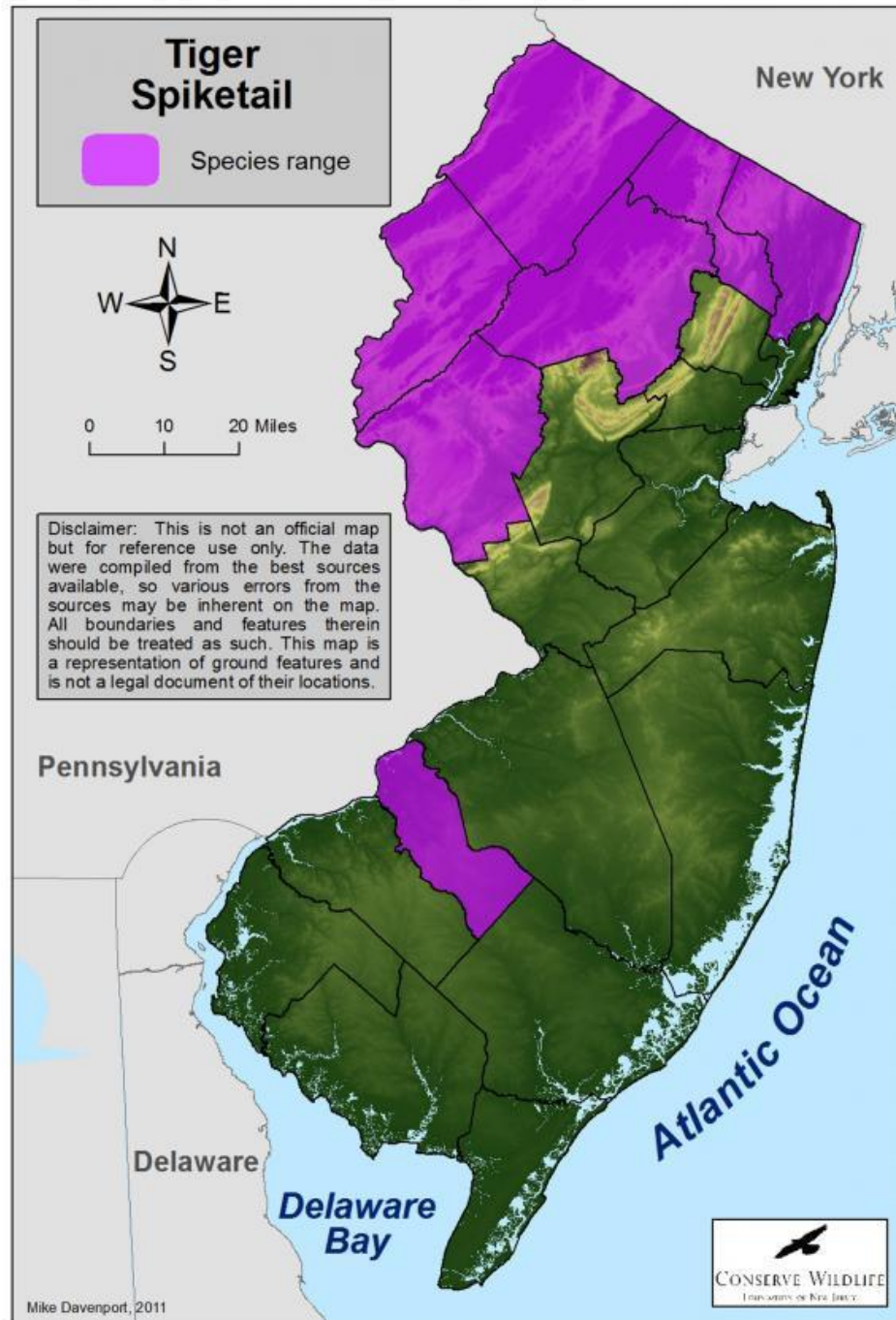


Figure 7. New Jersey distribution of *Cordulegaster erronea*. Source: Bangma, J. 2006. NJODES: The dragonflies and damselflies of New Jersey. Tiger Spiketail species profile. Retrieved from <http://www.njodes.com/Speciesaccts/spiketails/spik-tige.asp> on June 30, 2015.

conservation and permitting decisions. The Landscape Project utilizes a predictive habitat model for *C. erronea* developed by the NJDEP (ENSP) that employs a 500-meter buffer around all known records (NJDFW 2012). This buffer distance was apparently somewhat arbitrarily selected by the ENSP biologists because “insufficient information exists in the scientific literature to support the designation of an occurrence area.” and “Due to the absence of literature concerning Odonate species’ spatial requirements, a 500 meter radius was formulated based upon the expert opinion of the biologist responsible for reviewing these species within the NJ Endangered and Nongame Species Program.” The radio-telemetry data from this research study was compared to the NJDEP predictive model for one of the study streams to test its validity. Based on the plotting of the radio-telemetry locations for all six males that were outfitted with micro-transmitters and then tracked, the 500-meter buffer may be an appropriate level of habitat protection as all of the data points fall within that buffer. However, further research is warranted. Kissling *et al.* (2014) note that radio-telemetry estimates of home range may under represent the actual extent due to limitations of short battery life and the impact from weight-induced behavioral changes

Based on the telemetry data, and the habitat characteristics, *C. erronea* is almost certainly highly sensitive to landscape changes that alter stream hydrology and reduce forest cover adjacent to breeding streams. *C. erronea* streams all share common characteristics including ground water seepage hydrology and extensive adjacent mature forest (Barlow 1995; Glotzhober 2006). This is consistent with reports of many other Cordulegastridae (IUCN 2015, NatureServe 2015, Silsby 2001) and suggests that conservation strategies may be broadly employed for the family. The forest canopy is used extensively by both

sexes of *C. erronea* and likely plays an important role in maintaining the larval habitat. Based on this research, protection strategies for *C. erronea* should focus on the maintenance of large contiguous forested areas adjacent to breeding streams and the protection of groundwater seepages. Mark-resighting data (Chapter 4) show movement of *C. erronea* between streams separated by approximately 500 meters of contiguous forest. In our study, and as reported by Barlow (1995), Tiger Spiketails moved between streams, suggesting that maintaining forested connectivity between breeding streams is also important. *C. erronea* habitats are also used by other odonates of conservation concern and conservation strategies should protect a broad suite of other species.

Unfortunately, current New Jersey environmental regulations, while among the strongest in the nation, do not seem suitable for protecting *C. erronea* habitats. The New Jersey Freshwater Wetlands Protection Act (NJAC: 7-7A) provides a maximum wetland buffer width of 150-feet. Similarly, the New Jersey Flood Hazard Rules (NJAC 7:13) provide a maximum stream buffer of 150-feet. Some *C. erronea* streams may also receive a 300-foot buffer pursuant to the NJDEP Special Water Resource Protection Areas but even this expanded buffer is not likely wide enough to insure connectivity between metapopulations. Proposals in New Jersey to repeal or lessen this buffer have also been initiated and are pending. Based on this research, it is strongly recommended that all *C. erronea* streams are provided the maximum possible buffers and that conservation priorities target landscape-wide land protection measures.

LIFE HISTORY/ECOLOGY

Cordulegaster species are semi-voltine or parti-voltine, with larval stages taking from 2–

5 years to reach maturity (Burcher and Smock 2002, Corbet *et al.* 1999, Corbet, *et al.* 2006, Ferreras-Romero and Corbet 1999, Glotzhofer 2006, Marczak *et al.* 2006). *Cordulegaster* larvae are shallow burrowers (Corbet 1999) and are dependent upon specific microhabitats within their breeding streams and seepages (Boda *et al.* 2015, Corbet 1999). A combination of factors appears to be important including sediment size and composition, water quality, current, and geology (Hager *et al.* 2012, Marczak, *et al.* 2006; Müller and Waringer 2001, Tamm 2012, Weihrauch 2003). *Cordulegaster* habitats all share many common characteristics including largely undisturbed landscapes and extensive mature forest surrounding the breeding streams. For most species, studies are limited to a single location. While the ecology of a few European species has been well studied, the North American fauna has received much less attention. In North America, the few extensive studies of *Cordulegaster* include *C. erronea* in Ohio (Glotzhofer 2006), Say's Spiketail (*Cordulegaster sayi* Selys) in Georgia (Stevenson *et al.* 2009), Apache Spiketail (*Cordulegaster diadema* Selys) in Arizona (Alcock 1985), Twin-spotted Spiketail (*Cordulegaster maculata* Selys) in Virginia (Burcher and Smock 2002), Delta-spotted Spiketail (*Cordulegaster diastatops* Selys) and Twin-spotted Spiketail (*Cordulegaster maculata*) in New York (Hager *et al.* 2012) and the Pacific Spiketail (*Cordulegaster dorsalis* Hagen) in British Columbia (Marczak *et al.* 2006). However, only Glotzhofer (2006) and Stevenson *et al.* (2009) focused on the adults.

In New Jersey, *C. erronea* occurs in widely scattered populations across the northern tier of the state, and in a recently discovered disjunct population in southern New Jersey (Bangma 2006) (Figure 7). These habitats feature cold, spring and seepage fed streams flowing through extensive mature forest. The behavior of *C. erronea* is typical of the

genus, being an elusive species away from its breeding stream where only the males are easily observed while patrolling. Females are much less frequently observed at the breeding stream appearing only briefly to oviposit. Little is known about the habitat use of either sex away from the breeding stream. Observations of both sexes away from the stream are rarely reported. This research indicates that much of the time spent away from the breeding stream by both sexes is in the canopy (Glotzhober 2006). Prior to this study, mating, and the emergence location of the larvae, had not been reported. *C. erronea* is almost certainly highly sensitive to landscape changes that reduce forest cover adjacent to breeding streams and that alter stream hydrology. These streams all share common characteristics including ground water seepage hydrology and extensive adjacent mature forest (Barlow 1995, Glotzhober 2006). These habitats may be particularly sensitive to disturbance. Removal of forest cover has been shown to significantly alter stream hydrology (Hornbeck *et al.* 1970, Thorton *et al.* 2000). Small headwaters streams may also be more susceptible to increased temperature impacts than larger streams (Swift and Messer 1971). Forest clearing and riparian zone impacts can also affect aquatic insects, and small headwaters streams may be particularly sensitive (Gage *et al.* 2004). Gage *et al.* (2004) found substantially higher numbers of Cordulegastridae larvae in streams with low impacts compared to those with high impacts.

Based on the research, using a combination of study techniques including marking studies, radio-telemetry with micro-transmitters, lengthy observation periods, and larval and exuvial sampling, *C. erronea* possess an interesting suite of behavioral and ecological characteristics. They exhibit parti-voltinism and possibly a split cohort that is semi-voltine. The males are, long-lived, non-territorial and largely non-aggressive to

conspecifics; visit the streams only to patrol; patrol for relatively short periods throughout the day; patrol only a limited number of times during the day; search methodically for females; rarely feed at the streams; and except when patrolling, are in the canopy. The females, appear at the streams very infrequently, throughout the day, and typically only for short periods; may appear anywhere along the stream; oviposit in secluded places for long periods; were never observed feeding, and when not ovipositing are also in the canopy.

The larvae, based upon exuvial collections in New Jersey, Connecticut and Delaware, commonly emerge on trees, often at distance from the stream and elevated above the ground. The head width and encrusted nature of *C. erronea* exuviae and the size of the larvae in October and April suggests that *C. erronea* may be a “spring species” (Corbet 1952, Corbet 1957, Corbet 1964) with winter diapause in multiple instars. Emergence appears to be somewhat synchronized, largely during late-June to mid-July with long adult longevity resulting in a prolonged flight period.

Until recently, tracking the long-range movements of individual insects was not possible, but the advent of miniature radio-transmitters has now provided that opportunity. The radio-telemetry data from this study is the first obtained for *C. erronea* or any other Cordulegastridae species and despite potential limitations provides a deeper understanding of its life history than was previously available.

In New Jersey (and likely throughout most of the northeast), populations of the Tiger Spiketail have almost certainly declined from development and the conversion of forest to agriculture. A significant portion of the New Jersey range falls within some of the

wealthiest counties in the country, creating residential development pressures (USCB 2015). The state is also facing many new, above and below-ground utility lines and upgrades, and other infrastructure pressures (NJDEP 2015). The range of the Tiger Spiketail also corresponds to mountaintop mining and the extensive recent development of the Marcellus shale natural gas reserves and associated distribution pipelines, activities that may impact the high quality streams required by the species (Olcott 2011). The Tiger Spiketail has also been ranked as having High Regional Vulnerability suggesting that a regional conservation strategy is necessary to insure its protection (White *et al.* 2014).

Study Sites

This study was conducted at two *C. erronea* breeding streams on the Schiff Reservation Natural Lands Trust in Mendham Township, Morris County, New Jersey (40.764470, -74.620918). The streams are located at the bottom of broad forested valleys in the Highlands Physiographic Province of New Jersey. The Highlands Physiographic Province is characterized by a series of flat-topped ridges composed of crystalline, igneous, and metamorphic rocks separated by deep narrow valleys underlain by less resistant limestone and shale (Robichaud and Buell 1983).

Both streams are perennial headwaters fed by numerous groundwater seepages and are separated by a forested topographic divide of about 500 meters. The more easterly stream is approximately 1,200 meters in length and is approximately 1-3 meters wide. The second, more westerly stream, is approximately 600 meters long. Most of the stream has a well-defined channel ranging in width from about 1-3 meters. There is also a broad rocky area with a poorly-defined channel that is approximately 5 meters wide. Both

streams have interspersed sand, gravel and silt bottoms. Water depths in the streams rarely exceed 0.3 meters. Both streams flow through mature, mixed-deciduous forest. Undercut banks and overhanging vegetation characterize the streams and skunk cabbage (*Symplocarpus foetidus* (L.) Salisb. ex W.P.C. Barton) is scattered within and along the channels and in the many seepages that feed them. The streams are consistent with other *C. erronea* breeding streams in New Jersey (Barlow 1995, pers. obs. Moskowitz), Ohio (Glotzhober 2006), New York (NYNHP 2012) and elsewhere in the range (Needham et al. 2000, pers. obs. Moskowitz). As part of the study, many other *C. erronea* habitats were also visited in New Jersey, New York, Connecticut and Delaware.

OUTLINE OF DISSERTATION

This Dissertation is focused on exploring the life history and behavior of the Tiger Spiketail including: larval characteristics and habitat; adult behavior and habitat; home range estimates; site fidelity; mating strategies, mate recognition and mating behavior; and the presence and behavior of the adults at the breeding streams. The research reports the first observed mating, the first use of radio-telemetry to track individual *C. erronea*, the first comprehensive study of the exuviae and detailed observations of many other life history and behavioral characteristics that were previously unreported or poorly-known. Recommendations for conservation strategies and habitat protection measures are also provided. It is hoped that this study can be used by resource managers to develop appropriate conservation and habitat protection strategies for the species.

Objectives and Questions

In Chapter 2, I investigate the seasonal and spatial distribution of the larvae of *C. erronea*

through larval and exuvial sampling. Habitat characteristics were analyzed through Geographical Information System (GIS) mapping to understand life history aspects related to landscape attributes. Recommendations for conservation strategies are also presented.

In Chapter 3, I investigate *C. erronea* adult movement via radio-telemetry utilizing micro-transmitters to define habitat use and to estimate home ranges of individual dragonflies. This is the first application of radio-telemetry to *C. erronea* or any other Cordulegastridae and one of only a few for any dragonfly.

In Chapter 4, I investigate mating and mate recognition in *C. erronea* by presenting a suite of models and living and dead dragonflies to patrolling males. A supplemental video is available on YouTube at (<https://www.youtube.com/watch?v=cMPru3zihmQ>).

In Chapter 5, I investigate the use of the breeding streams by *C. erronea* through extensive marking studies to explore male patrolling, site fidelity, longevity, female oviposition and other behaviors.

A complete bibliography is also provided.

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Chapter 2

Larval Ecology, Habitat, and Emergence Site Selection of the Tiger Spiketail Dragonfly (*Cordulegaster erronea* Hagen) in New Jersey with Implications for ConservationDavid Moskowitz¹ and Michael L. May²**Abstract**

The Tiger Spiketail (*Cordulegaster erronea* Hagen) is of conservation concern in many states throughout its range and is likely highly susceptible to habitat impacts. Yet only a single study on the larvae has been conducted, in Ohio, and many life-history aspects are poorly understood. The present study evaluated the size, age structure and density of *C. erronea* larvae at a stream on the Schiff Reservation Natural Lands Trust (Schiff) in Mendham Township, Morris County, New Jersey. The habitat and surrounding landscape characteristics of this stream and a second *C. erronea* stream at Schiff were also investigated. One hundred thirty-seven *C. erronea* larvae were collected and measured during this study, 82 in the spring and 55 in the fall, representing pre- and post-adult emergence. Twenty-four exuviae were also found along both New Jersey study streams. An additional eight exuviae were found along two other streams in New Jersey and Connecticut. We are aware of only one other published report of a single *C. erronea* exuvia. The data and habitat assessment suggests *C. erronea* is parti-voltine and dependent upon high quality, fish-free, perennial headwaters streams flowing through extensive forest. The information obtained from this study may assist resource managers in developing conservation strategies and habitat protection measures for this species.

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Key Words: Odonata, dragonfly, *Cordulegaster erronea*, exuviae, life history, phenology, habitat, New Jersey.

Introduction

Cordulegaster (Leach) species are semi-voltine or parti-voltine with long larval stages taking from 2–5 years to reach maturity (Burcher and Smock 2002, Corbet et al. 1999, Corbet, et al. 2006, Ferreras-Romero and Corbet 1999, Glotzhober 2006, Marczak et al. 20006). *Cordulegaster* larvae are shallow burrowers (Corbet 1999) and are dependent upon specific microhabitats within their breeding streams and seepages (Boda et al. 2015A, Corbet 1999). A combination of factors appears to be important including sediment size and composition, water quality, current, and geology (Hager *et al.* 2012, Lang 2000, Marczak *et. al.* 2006, Müller and Waringer 2001, Tamm 2012, Weihrauch 2003). For most species, larval studies are limited to a single location.

Recent studies have explored larval life history aspects for Say's Spiketail (*Cordulegaster sayi* Selys) in Georgia (Stevenson et al. 2009), Twin-spotted Spiketail (*Cordulegaster maculata* Selys) in Virginia (Burcher and Smock 2002), Delta-spotted Spiketail (*Cordulegaster diastatops* Selys) and Twin-spotted Spiketail (*Cordulegaster maculata*) in New York (Hager *et al.* 2012) and the Pacific Spiketail (*Cordulegaster dorsalis* Hagen) in British Columbia (Marczak *et. al.* 2006). Similar larval studies in Europe have investigated other *Cordulegaster* species (Ferreras-Romero and Corbet 1999, Müller and Waringer 2001, Liebelt *et al.*, 2010/2011).

Only a single study on the larvae of the Tiger Spiketail (*Cordulegaster erronea* Hagen) has been conducted, in Ohio (Glotzhober 2006), despite being listed as Threatened,

Endangered, Critically Impaired, Special Concern, or of Greatest Conservation Concern in many states throughout its range (NatureServe 2015). In New Jersey, the Tiger Spiketail is listed as a Species of Special Concern by the New Jersey Endangered & Nongame Species Program and has been assigned a New Jersey Natural Heritage State Rank of S2 - Imperiled.

The present study evaluated the size, age structure and density of *C. erronea* larvae at a stream New Jersey. The habitat and surrounding landscape characteristics of this stream and a second nearby *C. erronea* stream were also investigated. Extensive exuvial collections were also made at these streams and other streams in the region. The information obtained from this study may assist resource managers in developing conservation strategies and habitat protection measures for this species.

Study Location

The larval sampling study was conducted at one of two *C. erronea* breeding streams on the Schiff Reservation Natural Lands Trust in Mendham Township, Morris County, New Jersey (40.764470, -74.620918). Exuviae were searched for and collected along both breeding streams. The streams are separated by a narrow topographic divide of about 500 meters. One flows east and the other west into significantly larger streams (Figure 1). The larval sampling stream is an unnamed tributary of McVickers Brook and is a perennial headwater stream fed by numerous groundwater seepages. The stream continued to flow even during and extended drought. This stream is approximately 1,200 meters in length and approximately 1-3 meters wide. The stream bottom has interspersed sandy, gravelly and silty areas. Water depths are shallow, rarely exceeding 0.3 meters and flow can be

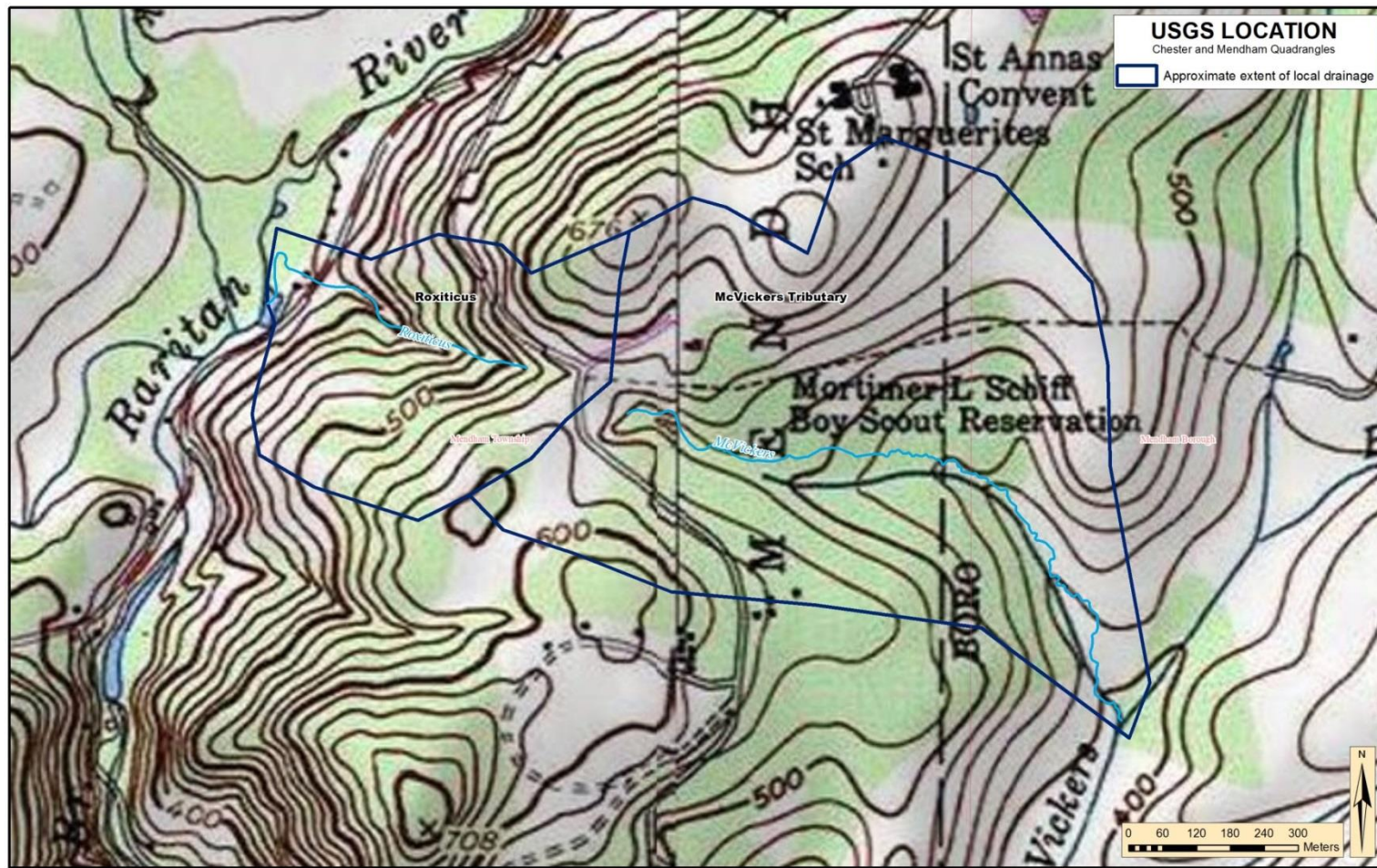


Figure 1. Location and topography of the study sites. Source: USGS Chester and Mendham, New Jersey Topographic Quadrangles. 1:24,000.

almost imperceptible. The stream flows through mature mixed deciduous forest that has remained uncut since at least 1930 based upon historical aerial photographs (Figures 2 and 3). Undercut banks and overhanging vegetation characterize the stream. Skunk cabbage (*Symplocarpus foetidus* (L.) Salisb. ex W.P.C. Barton) is scattered within the channel and in the many seepages that feed it. The second stream where exuviae were also found is an unnamed tributary to the North Branch Raritan River. This stream is also a perennial headwater stream fed by numerous groundwater seepages and is approximately 600 meters long. Most of the stream has a well-defined channel ranging in width from about 1-3 meters. There is also a broad rocky area with a poorly-defined channel that is approximately 5 meters wide. This stream also flows through mature mixed deciduous forest. Like the McVickers Brook tributary, the stream has undercut banks with overhanging vegetation and the bottom is interspersed with sandy, gravelly and silty areas. Skunk cabbage is also scattered within the channel and in the seepages that feed it (Figure 4). Water depths in this stream rarely exceed 0.1 meter with a nearly imperceptible flow. During a prolonged drought, the central portion of this stream was not flowing but the upper and lower portions were. Both streams are consistent with other breeding streams for *C. erronea* in New Jersey (Barlow 1995, pers. obs. Moskowitz), Ohio (Glotchober 2006), New York (NYNHP 2012) and elsewhere in the range (Needham *et al.* 2000).

Habitat Characteristics

Both *C. erronea* streams are located at the bottom of broad valleys in the Highlands Physiographic Province of New Jersey. The Highlands Physiographic Province is characterized by a series of flat-topped ridges composed of crystalline, igneous, and



Figure 2. 1930 aerial photograph of the study streams. Source: NJDEP 2015. New Jersey Department of Environmental Protection (NJDEP), Office of Information Resources Management (OIRM), Bureau of Geographic Information Systems (BGIS) 2005-02.



Figure 3. 2012 aerial photograph of the study streams. Source: NJDEP 2015. New Jersey Department of Environmental Protection (NJDEP), Office of Information Resources Management (OIRM), Bureau of Geographic Information Systems (BGIS).



Figure 4. Study streams. (Top) - McVickers Brook. (Bottom) - Unnamed Tributary of North Branch Raritan River.

metamorphic rocks separated by deep narrow valleys underlain by less resistant limestone and shale (Robichaud and Buell 1983).

According to mapping prepared by the New Jersey Department of Environmental Protection (NJDEP 2006), the surficial geology of the two study streams consists of alluvium and colluvium deposited in floodplains and the headwater areas of valleys underlain by weathered Gneiss (Figure 5). The bedrock geology as mapped by the NJDEP (1999) is primarily medium to fine-grained granite and fine to coarse-grained Gneiss (Figure 6). The NRCS (USDA 2008) has mapped soils consisting largely of the Edneyville-Parker-Califon Soil Series Association (Figure 7). The dominant Association soils are deep, excessively drained to somewhat poorly drained, gently sloping to steep, gravelly, sandy or stony loams weathered in place from bedrock or moved a short distance and redeposited in waterways. Minor soils range from well drained to poorly drained (Eby 1976). Field observations indicate that very poorly drained, mucky, highly organic soils also occur adjacent to the streams and seepages of the *C. erronea* habitats. The stream bottoms are sands and gravels with little organic matter (Figure 8). The two study streams have highly stable hydrology and even during an intense drought where the yearly rainfall total was approaching a twenty-five percent deficit, both continued to at least partially flow.

Methods

Tiger Spiketail larvae are highly cryptic and burrow shallowly in the sediment of streams and possibly seepages (pers. obs. Moskowitz; Glotzhober 2006). Unless they are moving they can be very difficult to discern from the sediments. The larvae area also densely

Figure 5. Surficial geology at the study streams. Source: New Jersey Department of Environmental Protection (NJDEP)/New Jersey Geological Survey (NJGS). 2006. Surficial Geology of New Jersey.

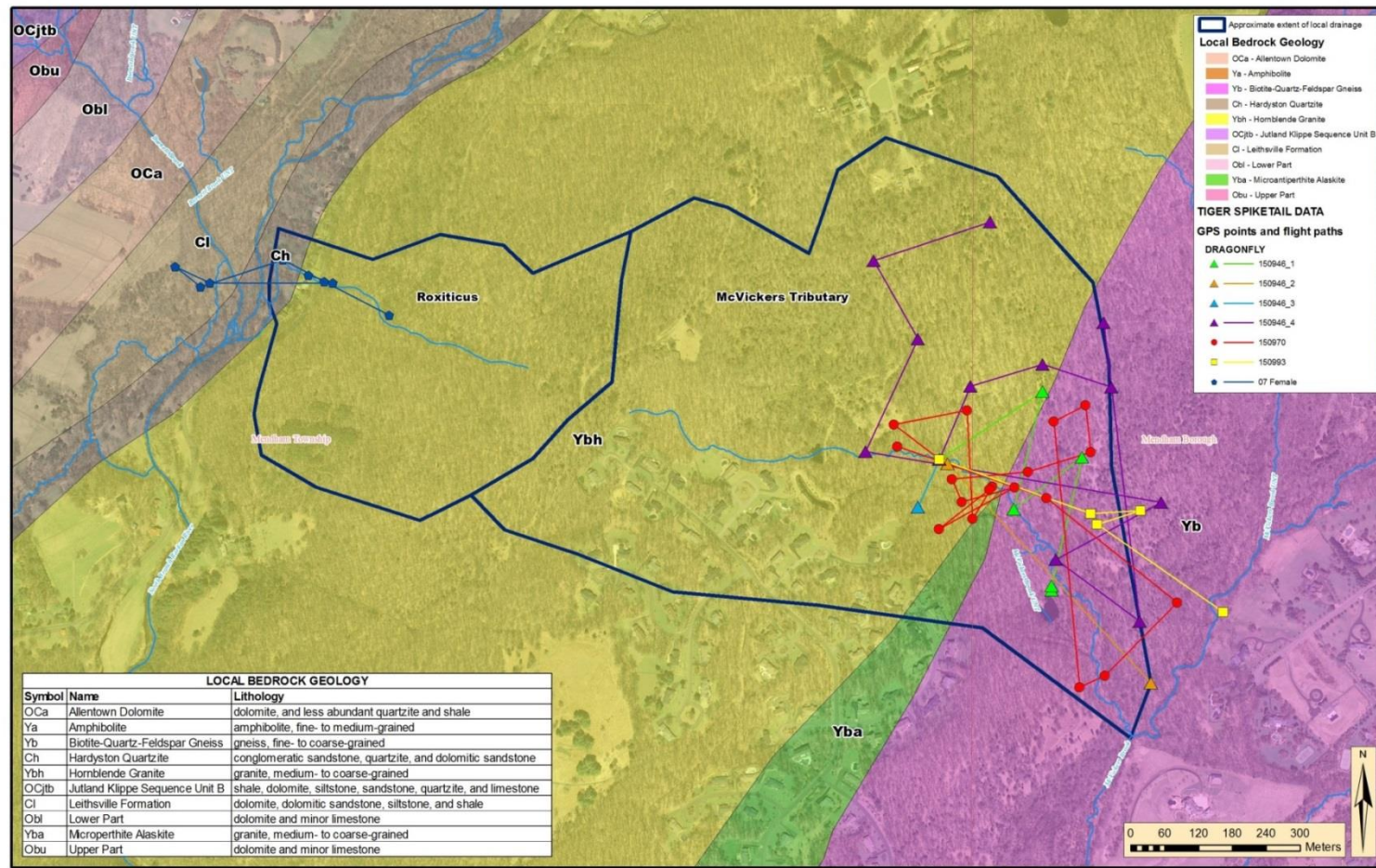


Figure 6. Bedrock geology at the study streams. New Jersey Department of Environmental Protection (NJDEP), New Jersey Geological Survey (NJGS). 1999. Bedrock Geology for New Jersey 1:100,000 Scale.

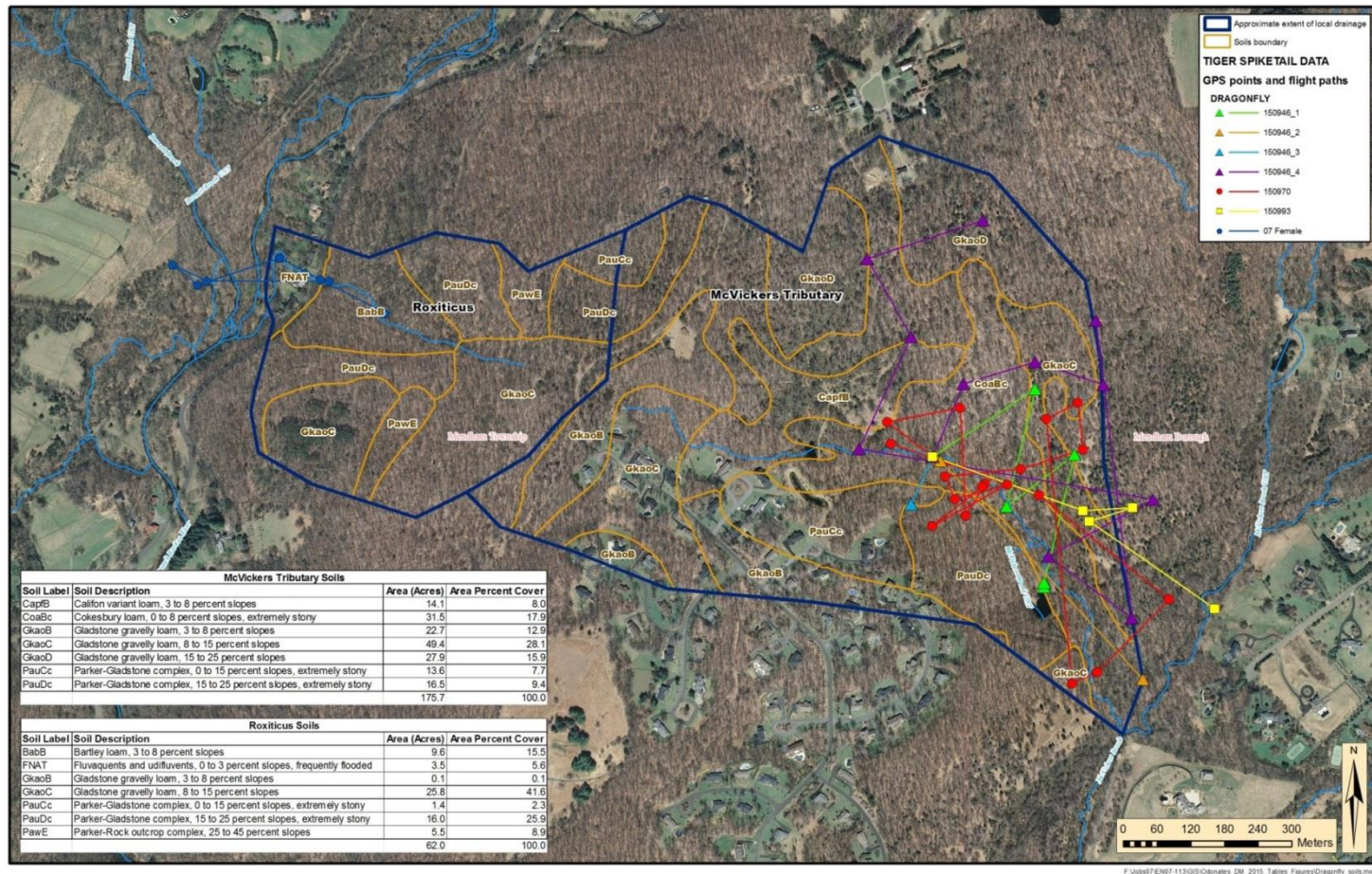


Figure 7. Soils mapping at the study streams. Source: U.S. Department of Agriculture, Natural Resources Conservation Service (USDA NRCS). 2008. Soil Survey Geographic 2008 (SSURGO) Database for Morris County, New Jersey (Projected to NJ State Plane Feet, NAD83). Version 20080818.



Figure 8. Typical stream bottom sediments of sand and gravel.

hairy and commonly coated with sand grains. In order to find *C. erronea* larvae for this study, the stream sediments were sifted through a 0.5 m x 0.5 m mesh-lined open frame box. The mesh was made of hardware cloth with 1 mm openings. Stream sediments were hand-shoveled into the mesh frame and then gently swirled with stream water to remove silt and other fine particles leaving only sand and cobbles behind. Using this method, the larvae were easily found amongst the remaining sediment including even very small individuals (Figure 9).

Larvae were sampled on 8 and 12 October and then again on 24, 25, 26 and 30 April in two 10-meter long study plots. The sample locations were in a different portion of the same stream in order to minimize any impacts from the October sampling upon the April sample. The April sample was located approximately 10 meters upstream of the October sample in order to minimize the potential for downstream movement of larvae between the two study periods. Both study plots appeared to exhibit similar characteristics. The April and October sampling dates were selected to understand pre- and post-emergence larval characteristics. An attempt was made to find every larva in the study plots by sampling all areas of loose sediment and gravel. Adults were observed flying on this stream from 1 July to 8 September, although exuviae found on 1 July indicate a flight period beginning in June (pers. obs. Moskowitz). In New Jersey the reported flight dates range from June 20 (May and Carle 1996) to 5 September (Bangma 2006). The sampling dates occur before and after these flight periods. The width of the stream at each 10-meter sampling location was measured at 1-meter intervals to obtain an average width for estimating larval densities.



Figure 9. (A). Sieve box used to sample for *C. erronea* larvae. (B). Various *C. erronea* instars collected in a single sample (C). Range of *C. erronea* instars found in the study stream.

In order to reduce stress and handling of the larva, measurements were made in the field using a hand-lens and estimated to the nearest half-millimeter. The maximum head width (HW) and total body length (L) for each larva was measured using the method described in Ferreras-Romero and Corbet (1999). The head width and body length were measured for each exuvia provided that the head and/or entire body existed. After each individual was measured it was released at the same location where it was collected.

Upon finding the first exuvia on 23 July, 2014, all trees within approximately 20 meters of the streams were searched regularly for additional exuviae until 12 August when none were found. The last exuviae were found on 30 July, 2014. Trees along the study stream were again searched for exuviae in July, 2015 and an additional 10 were found. When an exuvia was discovered, distance from stream, height above stream and tree species (or other location details if not on a tree) was recorded. *C. erronea* exuviae are readily identified by the distinctive spatulate setae on the frontal shelf and the shape of the epaulet (Needham, et al. 2000).

Results

An analysis of GIS data and field reconnaissance indicate the forested nature of both *C. erronea* study streams. Both streams flow predominantly through mature mixed deciduous forest. Aerial photographs from 1930 to the present show that the areas have been continuously forested. The approximate extent of the two watersheds inhabited by *C. erronea* was determined through a combination of the local USGS 7.5' topographic quadrangle and Digital Elevation Model. Land use/land cover (based on 2007 aerial imagery) and soils data were clipped to the approximated watershed boundary. The

drainage area of the McVickers Brook tributary is 71.2 hectares and for the unnamed tributary to the North Branch Raritan River, 25.1 hectares. Both streams have drainage basins that are largely wooded, the McVickers Brook tributary, 79.4% and the unnamed tributary, 95%. Single-family residential development was constructed within the McVickers Brook tributary drainage basin between 1995 and 2002 and comprises 15.7% of the area. Two single family homes are present in the drainage area of the unnamed tributary and comprise 5.2% of that drainage basin (Figure 10).

One hundred thirty-seven *C. erronea* larvae were collected and measured during this study, 82 in the spring and 55 in the fall (Figure 11). From the data collected, *C. erronea* is parti-voltine in New Jersey, as in Ohio (Glotzhober 2006). Both the April and October sampling periods, representing pre-and post-emergence of the adults indicated multiple sizes reflecting multiple age classes. Larvae in the spring had maximum head widths (HW) ranging from 2 mm to 8 mm (mean 3.94 mm \pm 2.0 mm) and total body length (L) ranging from 10 mm to 37 mm (mean 16.14 mm \pm 7.47 mm). Larvae in the fall had maximum head widths (HW) ranging from 1 mm to 8 mm (mean 5.15 mm \pm 1.32 mm) and total body length (L) ranging from 5 mm to 33 mm (mean 22.04 mm \pm 4.97 mm).

In April, 24% (n = 20/85) of the larvae had a HW of 4.5 mm or less. By contrast, in October, 64% (n = 35/55) of the larvae had a HW of 4.5 mm or less. Based on a laboratory rearing study of 21 *C. erronea* larvae in Ohio, Glotzhober (2006) found the following HW measurement ranges and related stadia: F-O = 7.2 – 8.5, F-1 = 5.8 – 6.8, F-2 = 4.5 – 5.7, F-3 = 3.6 – 4.5, F-4 = 3.0 – 3.8, F-5 = 2.3 – 3.0, F-6 = 1.9 – 2.4, F-7 = 1.7 – 2.0. Glotzhober (2006) found in Ohio that head width is the most reliable character for determining size class distinctions for instars of *C. erronea* at F0, F1, and F2 and slightly

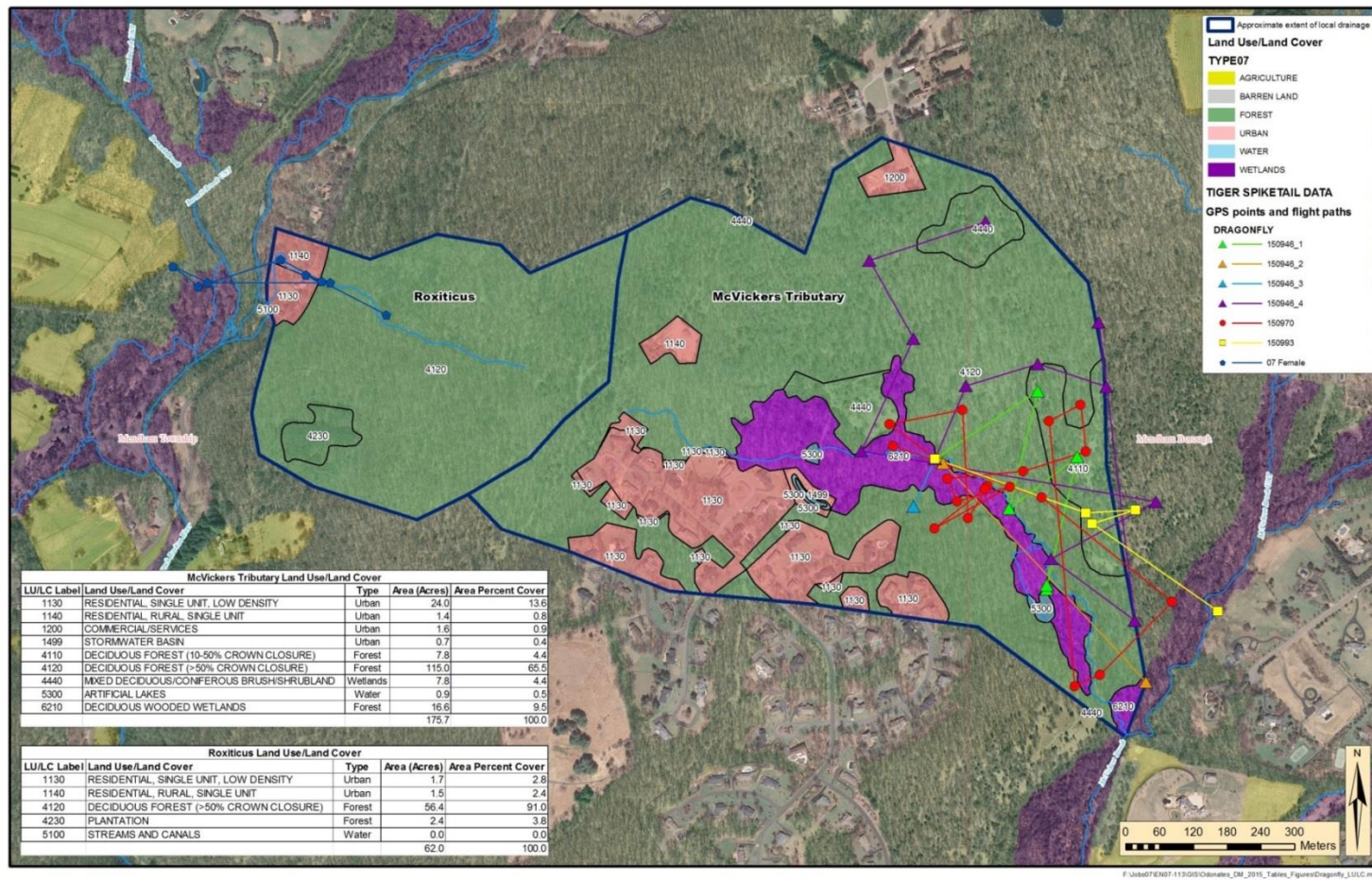


Figure 10. Land use and land cover at the study streams. Source: NJDEP 2015. New Jersey Department of Environmental Protection (NJDEP), Office of Information Resources Management (OIRM), Bureau of Geographic Information Systems (BGIS).

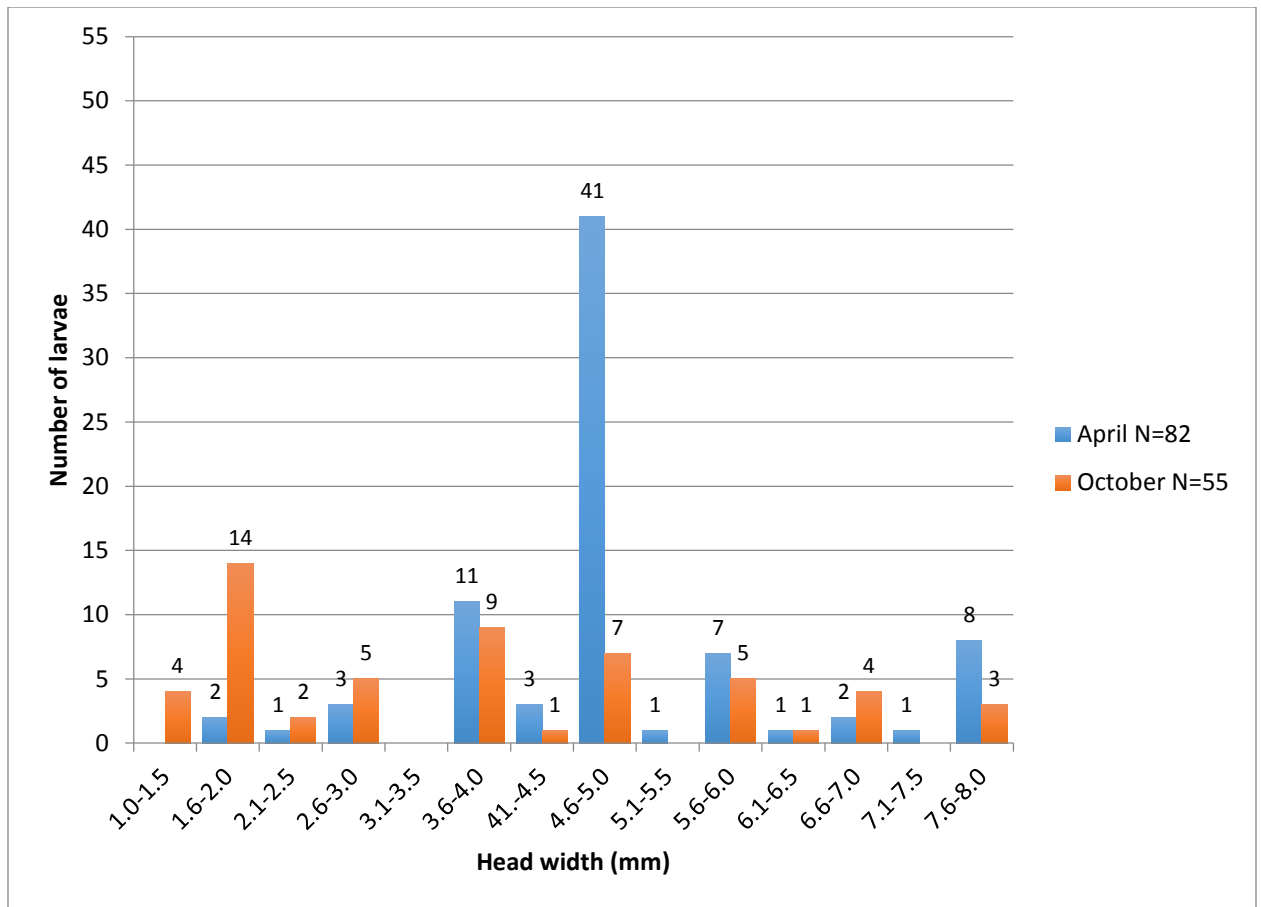


Figure 11. Head width (mm) of *Cordulegaster erronea* larvae from a stream in New Jersey. Per Glotzhober (2006) head width measurement ranges and related stadia: F-O = 7.2 – 8.5, F-1 = 5.8 – 6.8, F-2 = 4.5 – 5.7, F-3 = 3.6 – 4.5, F-4 = 3.0 – 3.8, F-5 = 2.3 – 3.0, F-6 = 1.9 – 2.4, F-7 = 1.7 – 2.0.

less distinct for F3 and F4 size classes. Glotzhober (2006) also found that total length is less useful for determining size class because larvae can stretch or compress the abdomen, resulting in variable measurements.

The data are consistent with the results of Glotzhober (2006) from Ohio for early instars but there were apparent differences in later instars. Given the small percentage (2.4) of larvae in the April sample with HW of 2.0 mm or less and the large percentage in October (32.8), these results are highly consistent with those of Glotzhober (2006). However, for later instars (F-0, F-2, F-3, F-4) the New Jersey spring sampling data differ. In Ohio, the largest percentage of the later instars (F-0 - F-4) in the spring sample was F-4 (28.4%), closely followed by F-3 (21%). F-2 larvae represented only 4.3 percent of the sample, with F-1 and F-0 each less than one percent. For the New Jersey spring data, F-2 had the largest percentage (51%) followed by F-3 (17.1%) and F-0 (9.8%) and then F-4 (3.7%). The percentage (45.5%) of individuals with smaller HW (1.0-3.0 mm) found in October, was not similarly observed in the April sampling (7.3%). This could indicate low winter survival rates or possibly continued growth during at least part of the period from October to April, as reflected in the large percentage (67.1%) of larvae with HW of 3.6-5.0 mm found in the April sample.

The two 10-meter stream segments sampled in an attempt to determine approximate larval density yielded 8 and 15 larvae, respectively. Assuming a similar distribution of larvae in the stream segments, the number of larvae per square meter of stream bottom ranged from one larva every 8.9 square meters to one larva every 11.6 square meters. Using the same distribution assumption, the number of larvae per linear meter of stream ranged from one larva every 0.67 meters to 1.25 meters with a mean of one larva every

1.10 meters. Glotzhofer (2006) found *C. erronea* in Ohio with a distribution of 1.25 to 1.43 larvae per linear meter. Lang *et al.* (2001) found 0.41 larvae per linear meter for *C. bidentata* and 0.78 larvae per linear meter for *C. heros* in Austria

Twenty-four exuviae were found along the streams at Schiff during the study (Table 1). Twenty were found on trees (Black birch (*Betula lenta* L.), Yellow birch (*Betula alleghaniensis* Britton), Red maple (*Acer rubrum* L.), American beech (*Fagus grandifolia* Ehrh.)), American elm (*Ulmus Americana* L.) and Sugar maple (*Acer saccharum* Marsh.), one was on Christmas fern (*Polystichum acrostichoides* (Michx.) Schott), two were on Barberry (*Berberis vulgaris* L.) and one was on the ground near the base of a tree. Of the 20 exuviae found on trees, 17 were on the trunk, two were on small branches and one was on a leaf (Figures 12 and 13). Twenty-two exuvia were found singly and two were on the same American elm approximately 31 cm apart. All but one exuvia was encrusted with sand grains and small pebbles and one was also heavily stained red (Table 2 and Figure 14). Encrusted exuviae have also been reported by Ferreras-Romero and Corbet (1999) for *C. boltonii* and for *Boyeria irene* (Fonscolombe) in Spain (Ferreras-Romero 1997). These authors suggest that encrusted and non-encrusted exuviae reflect parti-voltine and semi-voltine emergence, respectively.

Exuviae distance from the stream ranged from 76 cm to 518 cm with a mean distance of 222 cm \pm 124 cm. Their height above the ground was 229 cm with a mean of 132 cm \pm 60 cm. Four of the emergence trees were at the top of steep slopes that required the larvae to climb to reach the tree. Stream banks below the emergence sites were also often deeply undercut and nearly vertical requiring larvae to traverse these areas. Clearly, *C. erronea* larvae are proficient climbers. Emergence sites on trees and away from the water

Table 1. *C. erronea* exuviae emergence location and characteristics: (N=24)

Distance from Stream (cm)	Height Above Ground (cm)	Tree Species	Location
254	160	Black birch	On trunk
191	183	Not recorded	On trunk
130	On ground	Near Yellow birch	31cm from tree
160	86	-	On fern
259	191	Red maple	On trunk
325	97	Red maple	On trunk
427	180	Black birch	On trunk
285	155	Black birch	On trunk, up steep bank
76	61	Yellow birch	On trunk
158	71	Red maple	On trunk
396	109	Black birch	On trunk, up steep slope
122	160	American beech	On trunk
94	160	American beech	On leaf on short twig
226	208	American beech	On small branch
274	213	American beech	On trunk
152	97	American elm	On trunk
518	127	Yellow birch	On trunk
457	229	Sugar maple	On trunk
152	66	-	On Barberry
152	147	American elm	On trunk
159	71	American beech	On trunk
168	97	Red maple	On trunk
81	91	-	On Barberry
122	213	American beech	On small branch



Figure 12. *C. erronea* emergence location. Location of exuviae being pointed at.

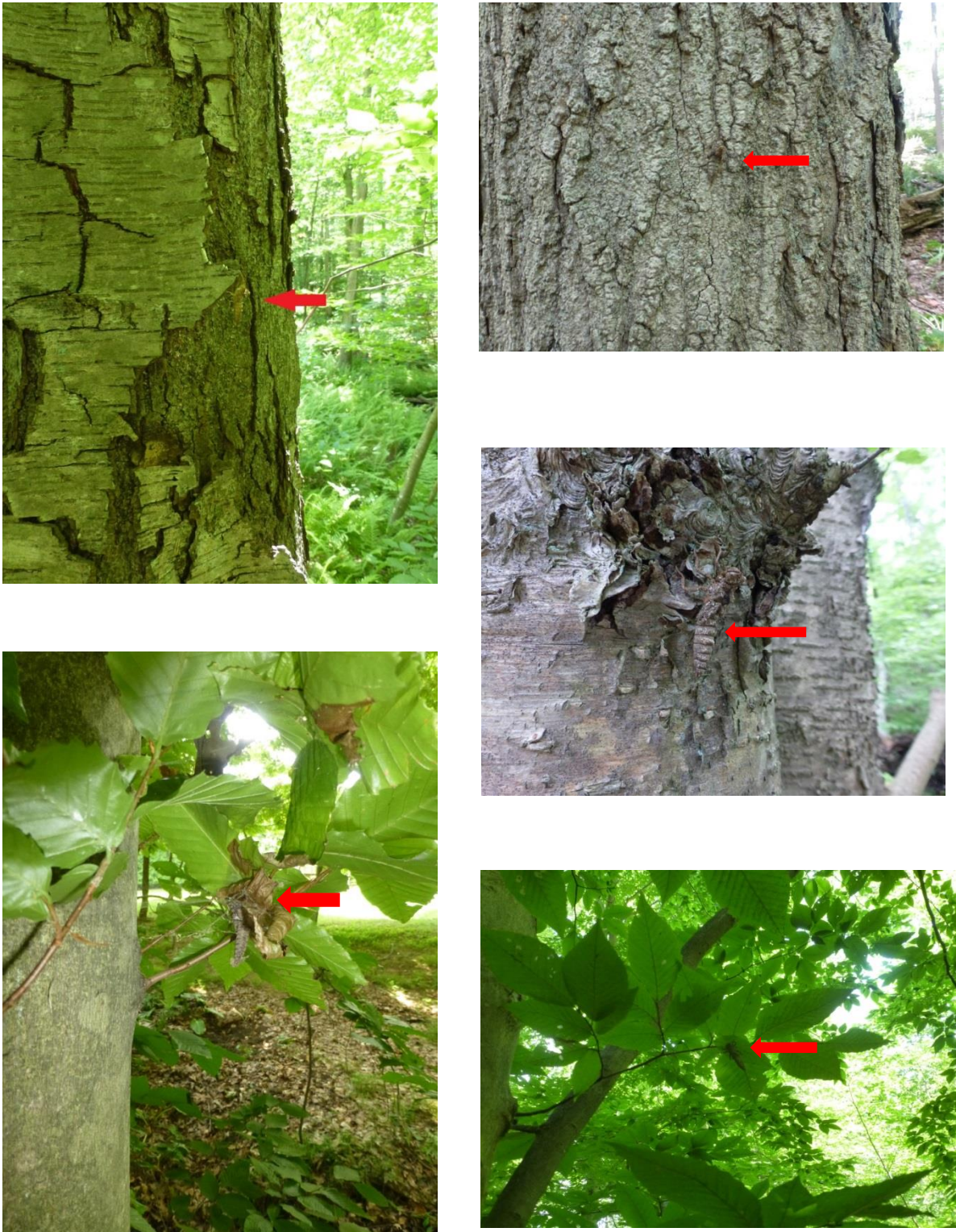


Figure 13. *C. erronea* emergence locations.

Table 2. Head width, body length and condition of *C. erronea* exuviae. (N=24)

Head Width (mm)	Body Length (mm)	Observations
8	37	Stained red
8	38	Lightly encrusted
7.5	38	Not encrusted
8	34	Lightly encrusted
8.5	38	Lightly encrusted
7 (estimated)	36	Head crushed, missing an eye, lightly encrusted
7.5	37	Lightly encrusted
-	-	No head and top of abdomen, lightly encrusted
7.5	-	No abdomen tip, lightly encrusted
8	37	Lightly encrusted
8	36	Lightly encrusted
8	35 (estimated)	Very bent, lightly encrusted
8	36	Heavily encrusted
8	-	No thorax or abdomen, heavily encrusted
8	38	Lightly encrusted
8	35	Not encrusted
8.5	40	Lightly encrusted
8.5	39	Heavily encrusted
8	37	Lightly encrusted
8	38 (estimated)	Heavily encrusted, abdomen very bent
8	38	Heavily encrusted
8	37	Heavily encrusted
9	38	Heavily encrusted
8	36	Lightly encrusted

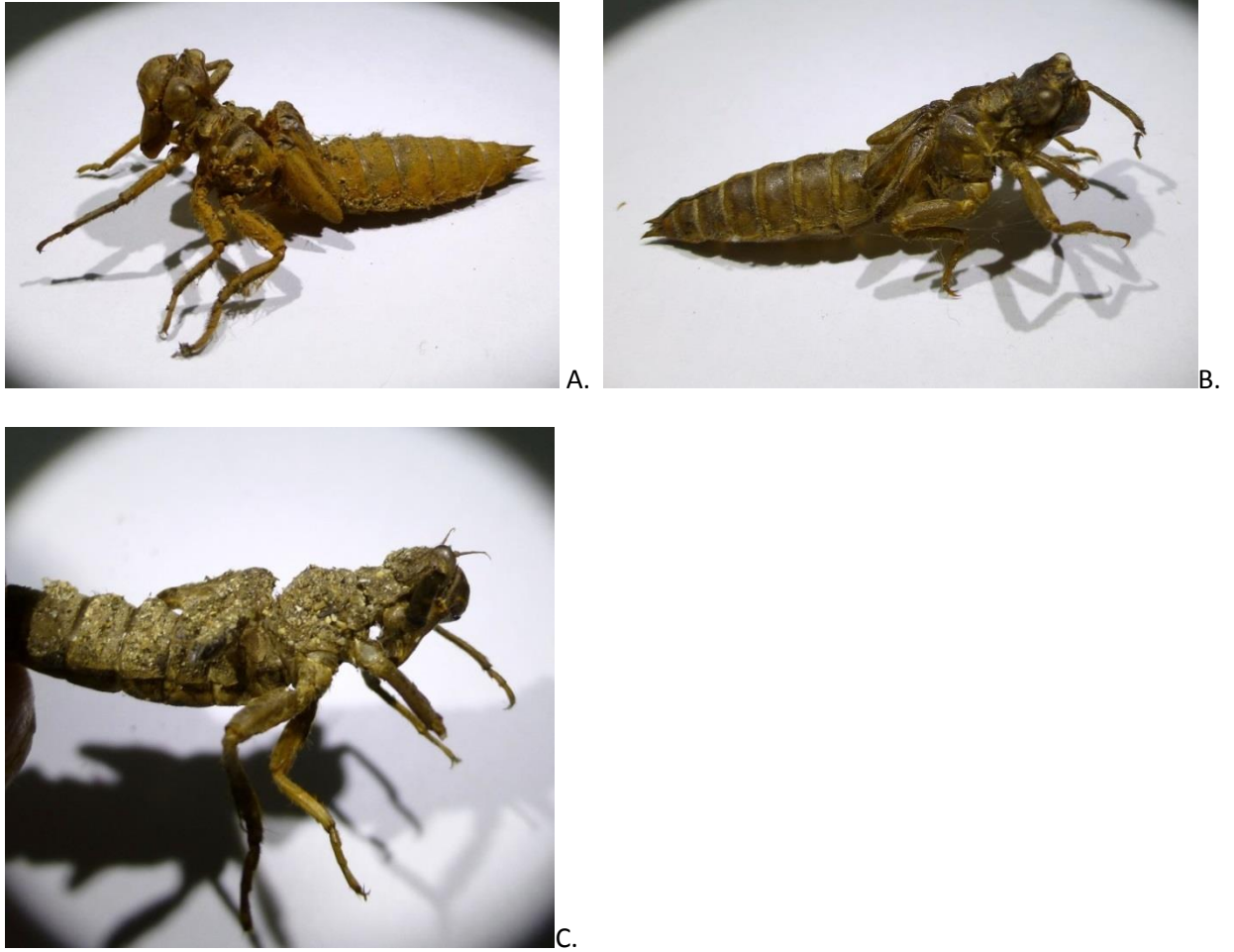


Figure 14. *C. erronea* exuviae. (A). Exuvia stained red. (B). Exuvia without encrustation. (C). Exuvia heavily encrusted.

appear to be broadly shared by other *Cordulegaster* species in North America including *C. dorsalis* in California (Kennedy 1917), *C. bilineata* in Tennessee, *C. maculata* (location not reported), *C. obliqua* in Wisconsin and *Cordulegaster sp.* in Quebec (as reported in Glotzhober 2006) and in Europe, including, *C. boltonii* in Germany (Weirauch 2003) and *Cordulegaster heros* (Theischinger) and *Cordulegaster bidentata* (Selys) in Germany (Muller 2000).

Various reasons have been proposed for emergence sites high above the ground including high larval densities (Bennett and Mill 1993, Corbet 1957), reducing predation (Coppa 1991, Miller 1964), reducing emergence site competition (Cordero 1995) and flooding (Worthen 2010). None of these seem applicable to *C. erronea*. Larval densities are low, high predation seems unlikely as amphibians and small mammals were rarely observed, emergence sites do not appear to be limited and the streams were never observed to flood. Trottier (1973) has also suggested climbing may reduce desiccation.

The head width of the exuviae ranged from 6.5 mm to 9.0 mm with a mean of 7.8 mm \pm 0.4 mm. Body length ranged from 34 mm to 40 mm with a mean of 37.1 mm \pm 1.4 mm. The size of the exuviae suggests that the larvae found in the April stream sampling event with head widths of 7.0 mm or greater emerged that summer. The October larval sampling event found no larvae with a head width of 7.1-7.5 mm but a small percentage (5.5%) with head width of 7.6-8.0 mm. This suggests that not all late instar larvae emerge each year. During both sampling periods various larval instars were collected in the study plots, reflecting an overlap of cohorts that is the result of the long larval period. This has also been reported for *C. erronea* in Ohio (Glotzhober 2006), *C. boltonii* in Spain

(Ferrerias-Romero and Corbet 1999) and *C. heros* and *C. bidentata* in Austria (Lang *et al.* 2001) and possibly *C. dorsalis* in British Columbia (Marczak *et al.* 2006).

The ability to find exuviae was tested by visits to other known *C. erronea* breeding streams. In late June, visits were made to two *C. erronea* streams, one in Fairfield County, Connecticut at the Trout Brook Valley Conservation Area and the other in Hunterdon County, New Jersey at the South Branch Reservation. A third stream at White Clay Creek State Park in New Castle County, Delaware was also visited in mid-July. At all three sites, all trees within approximately 10 meters of the streams were searched for exuviae. Nine exuviae were easily found during the searches; four each on trees along the New Jersey and Connecticut streams and one along the Delaware stream. All four exuviae along the Connecticut stream were on trees, two on sugar maple (*Acer saccharum* Marsh) and two on hemlock (*Tsuga canadensis* (L.) Carrière) and all were lightly to heavily encrusted with sediments. The distance from the stream for these exuviae ranged from 61 cm to 152 cm (mean = 122 cm \pm 37.3 cm). The height above ground ranged from 91 cm to 152 cm (mean = 130 cm \pm 5 cm). Each exuvia was measured and the head width ranged from 7.5 mm to 8.5 mm (mean = 8.1 mm \pm 0.4 mm) and the body length ranged from 36 mm to 40 mm (mean 38.0 mm \pm 1.6 mm). All four of the New Jersey exuviae were also found on trees along the stream; one on Black birch (*Betula lenta* [L.](#)), two on hemlock and one on American beech. All of the exuviae were lightly to heavily encrusted with sediments. The distance from the stream for these exuviae ranged from 31 cm to 777 cm (mean = 400 cm \pm 281 cm) and the height above the ground ranged from 76 cm to 152 cm (mean = 118 cm \pm 33 cm). Head width ranged from 8.0 mm to 8.5 mm (mean = 8.4 mm \pm 0.3 mm) and body

length ranged from 37.5 mm to 38 mm (mean 37.8 mm \pm 0.5 mm). The single exuvia found along the stream in Delaware was found on a Red maple 76 cm from the stream and 117 cm above the ground and was heavily encrusted. The head width and body length was not able to be determined as the exuvia was lacking the head.

Discussion

The head width and encrusted nature of *C. erronea* exuviae and size of the larvae in October and April suggests that *C. erronea* may be a “spring species” (Corbet 1952, Corbet 1957, Corbet 1964) with winter diapause in multiple instars. Emergence is largely during late June and July with long adult longevity resulting in a prolonged flight period. Only two exuviae were not encrusted or heavily stained. Fifty-eight percent (14/24) were lightly encrusted and 29 percent (7/24) were heavily encrusted. Whether this reflects a split-cohort with most larvae being parti-voltine and some semi-voltine as suggested for other species (Ferrerias-Romero 1997, Ferrerias-Romero and Corbet 1999) needs further investigation. Paulson and Jenner (1971) found that the distinction between “spring” and “summer” species in North Carolina may be poorly defined with a continuum between these life-history strategies. For *C. maculata*, they note there is a short, synchronized emergence but with overwintering in all the larger instars. They suggest this reflects the long development time of the larvae and may be a characteristic of all large odonates living in waters with low temperatures. Further work is likely needed to explore the larval development of *C. erronea* throughout its range given its patchy distribution across a broad geographic range. Higher elevation and latitude may affect the length of the larval period in *Cordulegaster* species and other odonates (Corbet *et al.* 2006, Ferrerias-Romero

and Corbet 1999, Glotzhofer 2006) and it would be interesting to investigate this in *C. erronea*.

The Tiger Spiketail is a species of conservation concern throughout its range. Only a single study has investigated the larval habitats (Glotzhofer 2006) and there are no published reports about exuviae (except a single exuvia noted in Glotzhofer 2006), potentially complicating conservation efforts. Exuviae may be of value for assessing life history aspects especially when the adults are not present at the breeding streams (Raebel *et al.* 2010). Foster and Soluk (2004) have noted for the federally-endangered Hine's emerald dragonfly, (*Somatochlora hineana* Williamson) that exuvial collections can provide reliable estimates of larval density and be of use for determining habitat quality. The same may be true for *C. erronea* given the relative ease of finding exuviae on trees near the larval habitats. Exuvial studies may also provide a strategy for habitat evaluations that do not impact larval populations (Raebel *et al.* 2010).

In New Jersey, the Endangered and Non-Game Species Program (ENSP) has developed a Landscape Project habitat model for *C. erronea*, but noted "Insufficient information exists in the scientific literature to support the designation of an occurrence area. In the Landscape Project, an occurrence area is the area a species needs to fulfill its life history requirements (breeding, resting, feeding)." (Winkler *et al.* 2008). In New York, an Element Distribution Model (EDM) for *C. erronea* was developed utilizing 44 potential habitat variables. The EDM identified the eight most important variables for potential habitat as topography, presence of water, slope, surficial geology, bedrock geologic class, percent shrub cover, percent wetland cover and May precipitation (Howard and Schlesinger 2012, NYNHP 2011). The predictive nature of this model for finding new *C.*

erronea sites is rated as fair (Howard and Schlesinger 2012). The limitations of the New Jersey and New York models suggest a better understanding of the larval habitats is necessary to refine the existing models or develop new models. In Germany, Tamm (2012) found that geology can be strongly predictive for *C. bidentata* and utilized for easily identifying larval and adult habitats.

Various factors may be useful for predictive models for *C. erronea*. The two larval streams are similar and are characterized as: perennial spring and seepage fed headwater streams that continue to flow during prolonged drought; in the uppermost reaches of the drainage basin; at the bottom of defined valleys; and flowing through large areas of mature forest. Fish were absent and other odonates were rarely encountered. These characteristics are similar to those in Ohio (Glotzhober 2006). With the exception of Ebony Jewelwing (*Calopteryx maculata* Palisot de Beauvois), which was commonly encountered and Clamp-tipped Emerald (*Somatochlora tenebrosa* Say) with about four males and two females noted in late August, the only other odonates observed during this study were limited to single individuals of Southern Pygmy Clubtail (*Lanthus vernalis* Carle), Mocha Emerald (*Somatochlora linearis* Hagen), Fawn Darner (*Boyeria vinosa* Say), Common Green Darner (*Anax junius* Drury) and Shadow Darner (*Aeshna umbrosa* Walker). No exuviae or larvae except *C. erronea* were encountered during this study. Only *S. tenebrosa* was observed ovipositing on the stream in mossy areas.

Given the broad conservation concern for *C. erronea*, a better understanding of the larval habitats is necessary to insure appropriate conservation and protection strategies. The range of the Tiger Spiketail and its habitat also corresponds to mountaintop mining and

the extensive recent development of the Marcellus shale natural gas reserves and associated distribution pipelines, activities that may impact the high quality streams required by the species (Olcott 2011). *C. erronea* has also been ranked as having High Regional Vulnerability suggesting that a regional conservation strategy is necessary to insure its protection (White *et al.* 2014). Barlow (2001) reported that a population of *C. erronea* in New Jersey was rapidly declining due to the removal of the surrounding forest canopy. Boda *et al.* (2015B) found that for *C. heros* vegetation composition and complexity appears to effect emergence behavior and recommend “maintaining riparian forests in near pristine condition.” This strategy is likely appropriate for *C. erronea* as the habitat may be particularly sensitive to disturbance given the headwaters location, spring-fed hydrology and occurrence in large, mature forest tracts, suggesting large riparian buffers and entire drainage basin protection may be needed to maintain habitat suitability.

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Chapter 3

Adult Tiger Spiketail (*Cordulegaster erronea* Hagen) Habitat Use and Home Range
Observed Via Radio-Telemetry with Conservation RecommendationsDavid Moskowitz¹ and Michael May²**Abstract**

The Tiger Spiketail dragonfly (*Cordulegaster erronea* Hagen) is geographically restricted to the eastern half of North America, patchily distributed within the range and a habitat specialist of small spring and seepage fed headwater streams flowing through mature forest. These habitats are highly sensitive to disturbance and the Tiger Spiketail is of conservation concern throughout most of its range. Yet little is known about the habitat use of either sex away from the breeding stream hampering conservation strategies. In this study we use miniaturized radio transmitters for the first time to investigate the habitat use and home range of individual males and a female Tiger Spiketail in New Jersey. We also provide recommendations for habitat protection and conservation. Our studies suggest a dragonfly that is critically dependent upon mature forest and the small high quality perennial headwaters streams that flow through them. These habitats are particularly sensitive to disturbance. Except when patrolling and ovipositing, both sexes are in the canopy above the breeding stream and in the adjacent mature forest, indicating the inseparable linkage between the aquatic and forested terrestrial habitat for this species. Our observations also suggest that *C. erronea* occurs in a metapopulation of nearby streams in our study area suggesting that conservation of this species requires

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broad forest protection far beyond the breeding stream. In New Jersey, and in other places throughout the range, there are many potential pressures on these habitats and current regulatory protections are not likely suitable. These same habitats may also be important for other Odonate species of conservation concern suggesting that protection of *C. erronea* may benefit a suite of species. We hope the information obtained from this study can assist resource managers in developing conservation and habitat protection measures.

Key Words: Odonata, dragonfly, *Cordulegaster erronea*, life history, phenology, habitat, radio-telemetry, home range, conservation, New Jersey.

Introduction

The Tiger Spiketail dragonfly (*Cordulegaster erronea* Hagen) is of conservation concern throughout most of its range yet little is known about the habitat use of either sex away from breeding streams, information that is critical for developing appropriate conservation strategies. Obtaining this information is difficult because the Tiger Spiketail is an elusive species away from its breeding streams where only the males are easily observed while patrolling. Females are rarely observed at the breeding stream appearing only briefly to oviposit. Observations of both sexes away from these habitats are rarely reported. Anecdotal reports, and observations, suggest that much of the time spent away from the breeding stream by both sexes is in the canopy (Glotchober 2006). Nearly all of the North American *Cordulegaster* species are of conservation concern throughout all or

part of their range (NatureServe 2012). Most are also geographically restricted, patchily distributed within their range and habitat specialists (NatureServe 2015, Paulson and Dunkle 2009). Despite this, comprehensive life-histories for most *Cordulegaster* species are lacking and the existing studies are often limited to a single location. Nonetheless, similarities between various species suggest that conservation strategies may be broadly applied across the family.

Only two previous studies have explored the life history of *C. erronea*, in New Jersey (Barlow 1995) and in Ohio (Glotzhober 2006). Other studies have explored life history aspects of other Cordulegastridae including Say's Spiketail (*Cordulegaster sayi* Selys) in Georgia (Stevenson *et al.* 2009), Twin-spotted Spiketail (*Cordulegaster maculata* Selys) in Virginia (Burcher and Smock 2002), Delta-spotted Spiketail (*Cordulegaster diastatops* Selys) and Twin-spotted Spiketail (*Cordulegaster maculata*) in New York (Hager *et al.* 2012) and the Pacific Spiketail (*Cordulegaster dorsalis* Hagen) in British Columbia (Marczak *et. al.* 2006). Similar studies in Europe have investigated other *Cordulegaster* species (Ferrerias-Romero and Corbet 1999; Müller and Waringer 2001). Most of these studies are limited to a single location or geographic area.

Until recently, tracking the long-range movements of individual insects was not possible, but the advent of miniature radio-transmitters has now provided that opportunity. Radio telemetry has been successfully applied to study the movement of individual insects such as carpenter bees (Pasquet *et al.* 2008), beetles (Hedin and Ranius 2002, Riecken and Rath, 1996), Mormon crickets (Lorch *et al.* 2005), bumble bees (Hagen *et al.* 2011), and orchid bees (Wikelski *et al.* 2010). Only a few radio telemetry studies have been conducted on dragonflies; for migrating Common Green darners (*Anax junius* Drury)

(Wikelski *et al.* 2006) in New Jersey and Delaware, for the Emperor dragonfly (*Anax imperator* Leach) in Great Britain (Levett and Walls 2011) and for three species of dragonflies in Singapore: Forktail (*Macrogomphus quadratus* Selys), Pond Cruiser (*Epophthalmia vitigera* Rambur) and Stream Cruiser (*Macromia cincta* Rambur) (Jia and Wei 2012). Radio telemetry studies have also been used to determine the first quantitative estimates of the home range of individual insects for beetles (Sprecher-Uebersax and Durrer 2001), bumblebees (Hagen *et al.* 2011), Orchid bees (Wikelski *et al.* 2010) and crickets (Fornoff, *et al.* 2012). Levett and Walls (2011) also utilized radio telemetry to obtain home range estimates for *Anax imperator* in the only published study for odonates. In this study we use miniaturized radio transmitters for the first time to investigate the habitat use and home range of individual males and a female *C. erronea*.

Study Location

The radio-telemetry study was conducted at two *C. erronea* breeding streams on the Schiff Reservation Natural Lands Trust in Mendham Township, Morris County, New Jersey (40.764470, -74.620918). The streams are located at the bottom of broad forested valleys in the Highlands Physiographic Province of New Jersey. The Highlands Physiographic Province is characterized by a series of flat-topped ridges composed of crystalline, igneous, and metamorphic rocks separated by deep narrow valleys underlain by less resistant limestone and shale (Robichaud and Buell 1983).

Both streams are perennial headwaters fed by numerous groundwater seepages and are separated by a forested topographic divide of about 500 meters. The more easterly stream is approximately 1,200 meters in length and is approximately 1-3 meters wide with a

gravelly and silty bottom. The second, more westerly stream is approximately 600 meters long. Most of the stream has a well-defined channel ranging in width from about 1-3 meters. There is also a broad rocky area with a poorly-defined channel that is approximately 5 meters wide. Water depths in the streams rarely exceed 0.3 meters. Both streams flow through mature, mixed-deciduous forest. Undercut banks and overhanging vegetation characterize the streams and skunk cabbage (*Symplocarpus foetidus* (L.) Salisb. ex W.P.C. Barton) is scattered within and along the channels and in the many seepages that feed them. Both streams have highly stable hydrology and remained at least partially flowing during a prolonged drought. Stream sediments are interspersed sand, gravel and silt. The streams are consistent with other breeding streams for *C. erronea* in New Jersey (Barlow 1995, pers. obs. Moskowitz), Ohio (Glotzhober 2006), New York (NYNHP 2012) and elsewhere in the range (Needham et al. 2000, pers. obs. Moskowitz).

Materials and Methods

Six male and one female Tiger Spiketail dragonflies were outfitted with miniature radio-transmitters for this study. Each individual was fitted with a small, lightweight (200 mg, including the battery) radio transmitter (Blackburn Transmitters, c/o Philip Blackburn, Nacogdoches, TX - 2 radio pulses per second, frequency band-width 150.000-151.999 MHz, antenna length 76mm) attached to the ventral thorax using small amounts of a combination of eyelash adhesive (Andrea Glue, American International Industries, Commerce, CA) and superglue (Krazy Glue, Elmers, OH) (Figure 1). Dragonflies studied here were not weighed before the transmitters were attached to minimize handling and stress prior to release, but 5 other males from New Jersey weighed 0.482 to 0.626 g (0.560 g \pm 0.057 S.D) (M. May unpublished data).

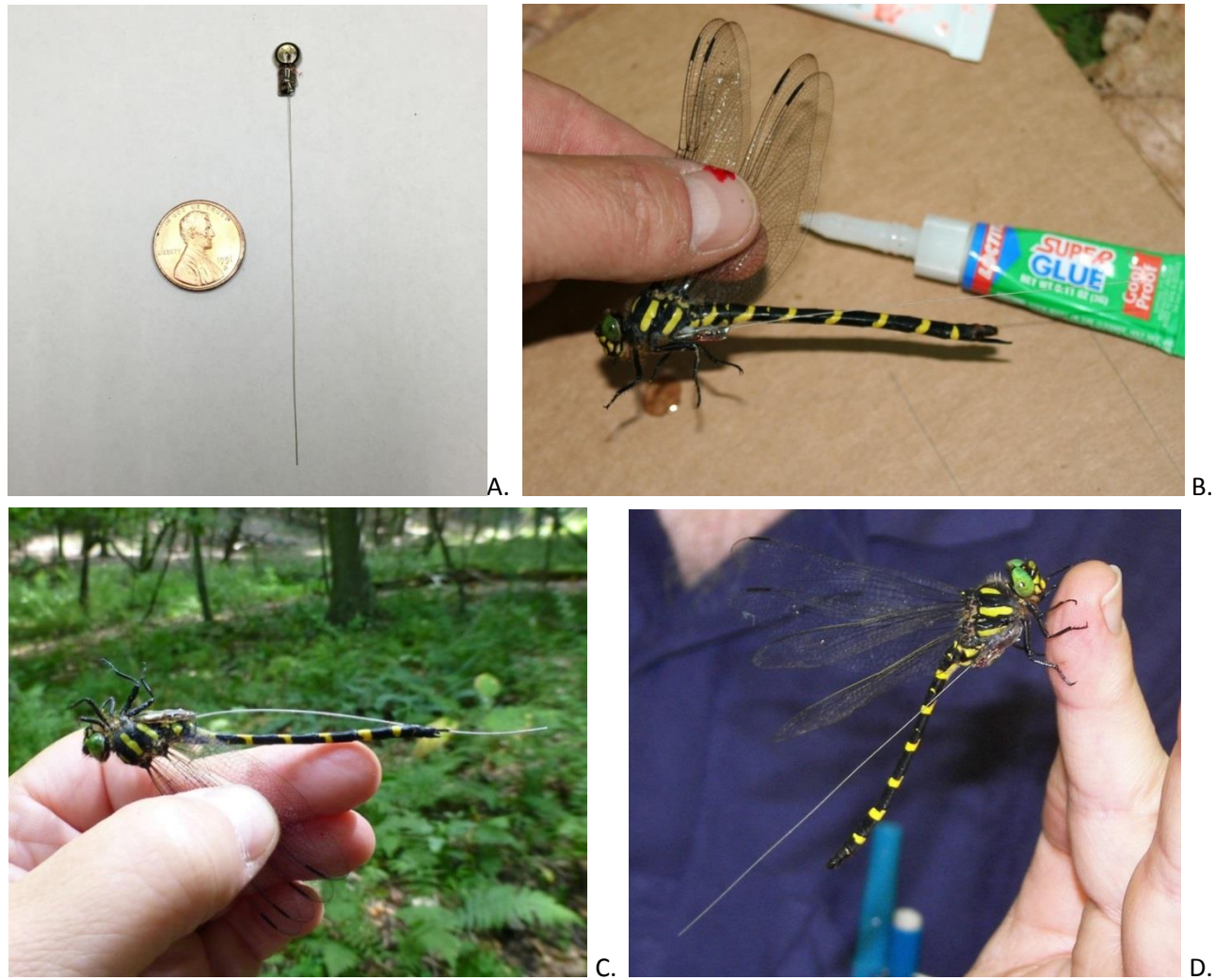


Figure 1. Micro-transmitter and attachment. (A). Micro-transmitter. (B). Transmitter attachment method. (C). Female *C. erronea* with transmitter attached. (D). Male *C. erronea* with transmitter attached.

In order to attach a transmitter, each dragonfly was held by the wings between two fingers with the wings over the thorax while the eyelash adhesive and glue was applied and the transmitter was gently pressed onto the thorax. This process typically took about 3 minutes, although the precise time was not recorded. Once the glue had set, and the transmitter was firmly attached, each dragonfly was placed on a finger and allowed to fly off when ready. Although the time lapse between this process and flight was not recorded, it was always less than one minute.

During the study periods the dragonflies were tracked on a daily or more frequent basis by one or two researchers using a YAESU VR-500 Communications Receiver (YAESU U.S.A. Cerritos, CA). Tracking continued until a dead dragonfly was found with the transmitter attached (one individual) or until the signal was lost (6 individuals). The life of the transmitters was rated at approximately 10 days but one transmitter was still active on day 17, after which the signal was no longer found. All dragonflies were radio-tracked at least once daily during the time that a signal could be obtained from the transmitter. Multiple observations on a single day were recorded for two of the males and the lone female (Figure 2).

The location of dragonflies in the canopy was approximately determined by using the receiver from various angles from the ground to obtain the strongest signal strength at a particular point. Precise coordinates for each location were determined using a handheld Garmin etrex GPS receiver (Olathe, Kansas). The radio-telemetry data was also used to obtain a potential home range for each individual dragonfly. The minimum convex polygon (MCP) method (White and Garrott 1990) was used to estimate home range sizes in ArcView GIS (Redlands, California). The MCP is the most common method of

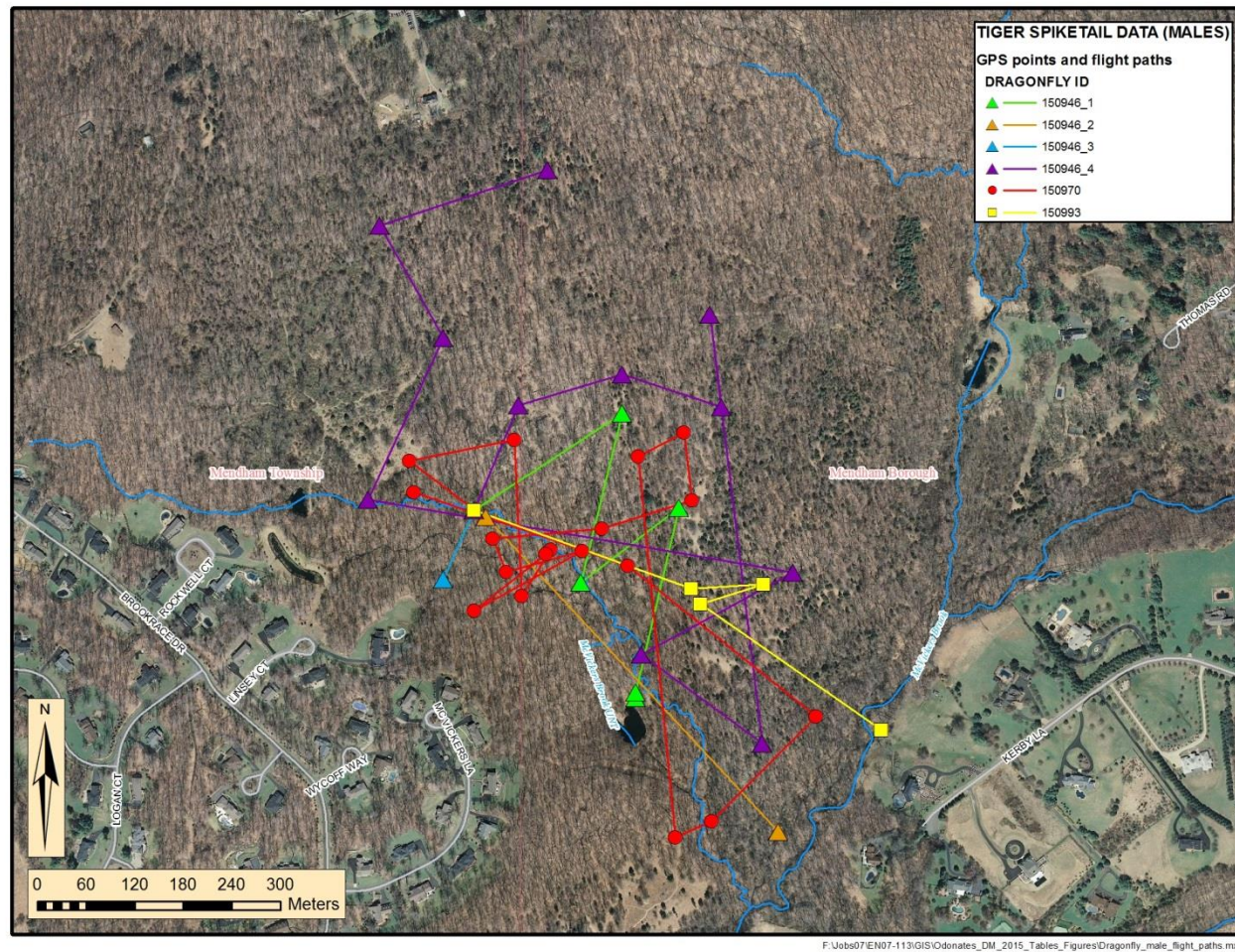


Figure 2. Radio-telemetry plotting of *C. erronea*.

estimating home range sizes (White and Garrott 1990) and is constructed by connecting the outer data point locations to form a convex polygon, and then calculating the area within this polygon (Kenward 1987).

The habitat analysis was conducted using Geographic Information System mapping. The approximate extent of the two watersheds inhabited by *C. erronea* was determined through a combination of the United States Geologic Survey 7.5' topographic quadrangle and Digital Elevation Model. Land use/Land cover (based on 2007 aerial imagery). Soils data were clipped to the approximated watershed boundary.

Results

Geographic Information System (GIS) data and field observations indicate that both study streams flow predominantly through mature, mixed-deciduous forest. Aerial photographs from 1930 to the present show that the areas have been continuously forested. The drainage area of the more easterly stream is 71.2 hectares and for the more westerly stream, 25.1 hectares. Both streams have drainage basins that are also largely wooded, the more easterly, 79.4% and the more westerly, 95%. Single-family residential development was constructed within the more easterly drainage basin between 1995 and 2002 and comprises 15.7% of the area. Two single family homes are present in the more westerly drainage area and comprise 5.2% of that drainage basin.

Each of the six males was followed with radio telemetry from 2 to 17 days (Mean = 6.2 +/- 5.7 S.D.). For the four males with more than two tracking days and therefore more than two data points, tracking ranged from 4 to 17 days (Mean = 8.25 +/- 6.0 S.D.). The

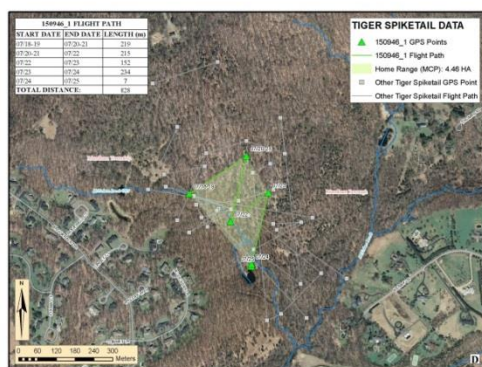
female was tracked for 3 days. Once a dragonfly was outfitted with a transmitter and released, all of the males flew away with a continuous upward rise into the canopy above the release point. This flight pattern appeared visually similar to the reaction of released dragonflies without a transmitter. Nonetheless, there was no way to quantify how the transmitter load may have impacted flight performance. The lone female that was part of this study flew to a nearby tree upon release and perched for about one minute before then flying off into the canopy. Only one male dragonfly was visually located after the initial release and only for a few seconds as it flew through the canopy.

Based upon the radio-telemetry, all of the dragonflies spent long periods in the canopy during the observation periods and often made long distance movements between observation periods. For the four males with more than two data points ($N = 37$), the movements ranged from 7.3 m to 533 m (Mean = 176 m \pm 126 m). The cumulative movement distances recorded for the male dragonflies ranged from 727 m to 2589 m (Mean = 1682 \pm 1044 S.D.). None of the males with a transmitter attached were re-found patrolling the breeding stream after the initial capture and release. One male was briefly seen flying through the canopy with the transmitter attached. The lone female left the study area and spent time in the canopy along a lower portion of the same stream near its confluence with a larger stream. It is possible that the dragonflies revisited the breeding streams during the study in between observation periods resulting in unrecorded movements.

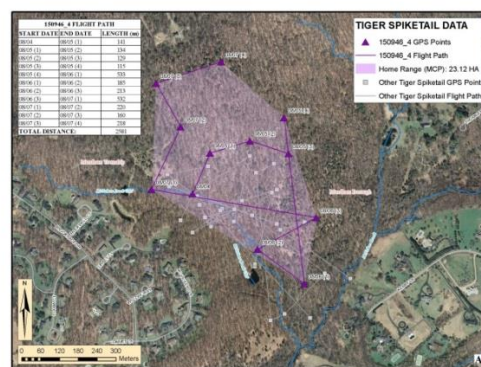
The estimated MCP home range for the four male dragonflies that had more than two data points was 2.55 ha to 23.12 ha (Mean = 11.13 \pm 9.6 ha). The two males with the largest number of data location points also exhibited the largest estimated home range (11

Table 1. Estimated Home Range Using Minimum Convex Polygon (MCP)

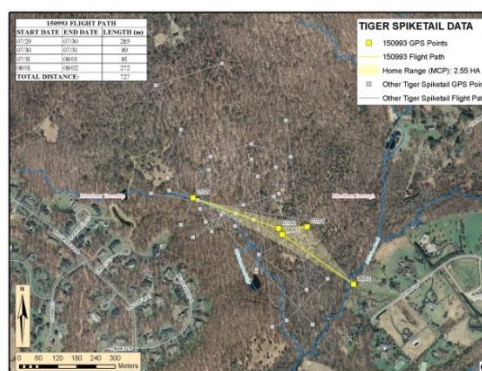
Dragonfly Frequency	Sex	No. of Data Points	Days Tracked	MCP Home Range (ha)
150.993	M	4	5	2.55
150.946-1	M	5	8	4.46
150.970	M	18	17	14.37
150.946-4	M	11	4	23.12
151.473	F	7	6	1.59



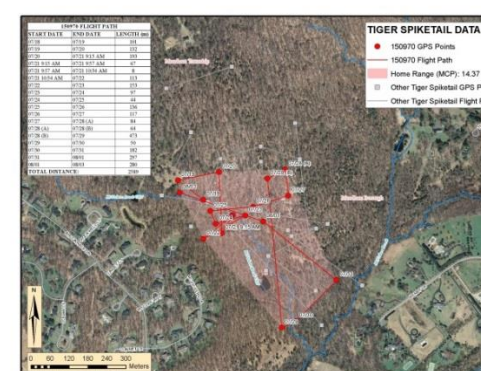
A.



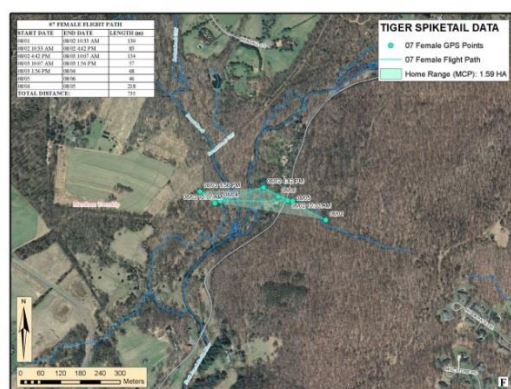
B.



C.



D.



E.

Figure 3. Radio-telemetry and home range plotting. (A-D). Male *C. erronea*. (E). Female *C. erronea*.

data points = 23.12 ha; 18 data points = 14.37 ha). The MCP for the lone female in this study was 1.59 ha. (Table 1 and Figure 3). The home range plotting for all of the dragonflies supports *C. erronea* as being a woodland species strongly associated with the breeding streams. The home range of all of the radio-tracked individuals was entirely within forested areas and bisected by the breeding streams. The home ranges of the individual dragonflies also overlap extensively, with virtually no indication of exclusive areas, suggesting a lack of territoriality (Figure 4).

The radio-tracking data was also used to construct movement distances between observation points, either daily or more frequently for five individuals (4 male, 1 female) on one or two days (Table 2). These movements ($n = 40$) ranged from 7.0 to 533 meters (mean = 176 m S.D. \pm 127.5 meters). For the female, 7 data points were obtained with a movement distance ranging from 46 to 218 meters (mean = 108 meters S.D. \pm 63 meters).

Discussion

Little is known about the habitat use of *C. erronea* away from the breeding stream (Glotzhober 2006; NJDEP 2012, 2012b) or the movements and home range of individual dragonflies (Dolny 2014, Levett and Walls 2011; Wikelski *et al.* 2006) information that is critical for developing appropriate conservation strategies. In New Jersey, the Tiger Spiketail was recently listed as a Species of Special Concern by the New Jersey Endangered & Nongame Species Program and has been assigned a New Jersey Natural Heritage Rank of S2 – Imperiled (NJDFW 2015). The species is similarly rare to uncommon in other surrounding states and is listed as Threatened, Endangered, Critically

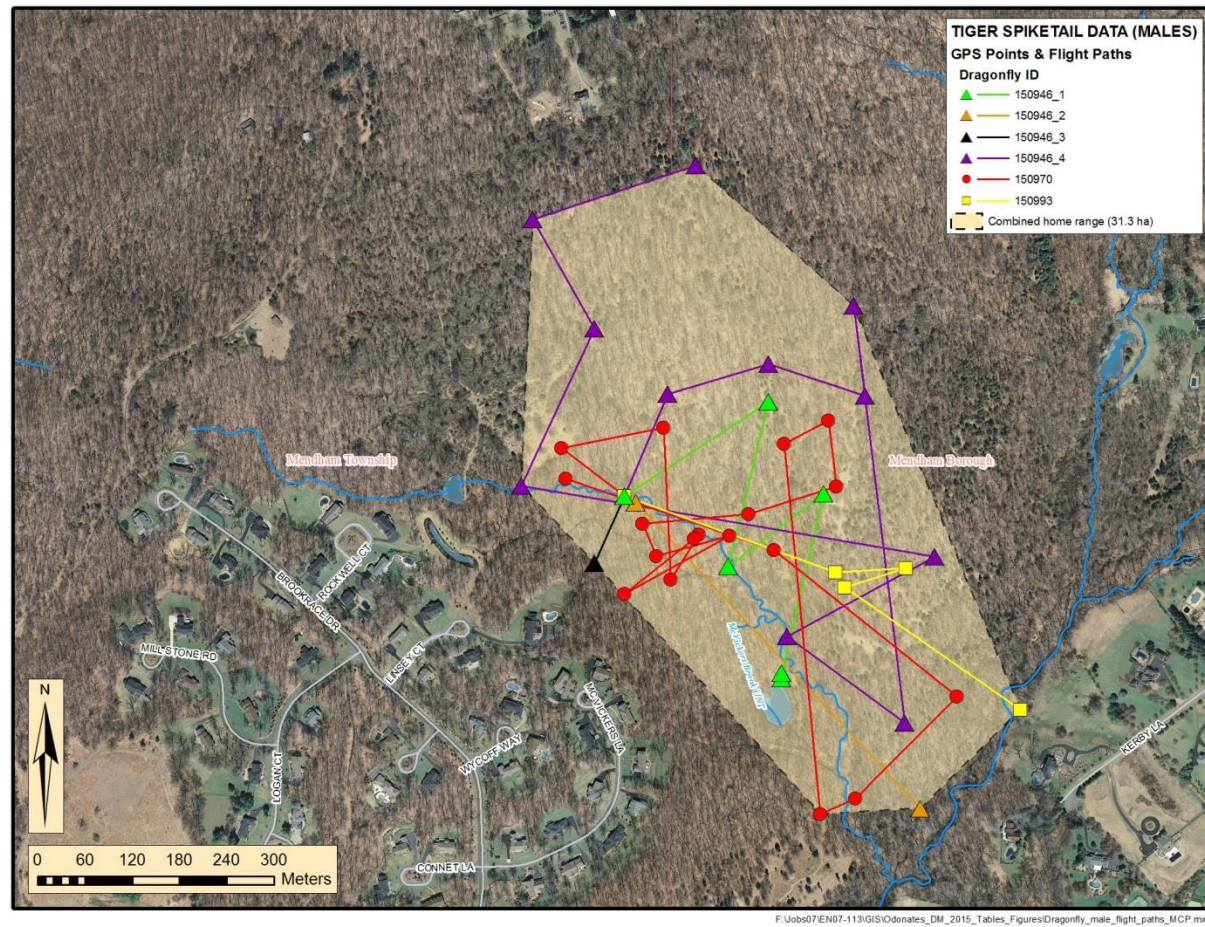


Figure 4. *C. erronea* combined home range plotting.

Table 2. Movement Distances for All Radio-tracked dragonflies.

Dragonfly	Sex	Data Points	Min. Movement (M)	Max. Movement (M)	Avg. Movement (M)
150.993	M	4	81	285	182 +/- 112 m
150.946-1	M	5	7.3	234	166 +/- 94 m
150.970	M	18	7.9	472	144 +/- 112 m
150.946-4	M	11	116	533	235 +/- 152 m
150.946-2	M	2	530	530	530
150.946-3	M	2	93	93	93
151.473	F	7	45	218	108 +/- 63 m

Impaired, Special Concern, or of Greatest Conservation Concern in many states throughout its range (NatureServe 2012). The information obtained from this study may assist resource managers in developing conservation and habitat protection measures.

In New Jersey the Tiger Spiketail is patchily distributed across the northern tier of the state and in a recently discovered disjunct population in southern New Jersey (Bangma 2006). The species has also been added to the New Jersey Landscape Project mapping, a species based mapping model that identifies habitats for rare species throughout the state (NJDFW 2012). This mapping utility is utilized by the NJDEP and other regulatory agencies for various land use, conservation and permitting decisions. The Landscape Project utilizes a predictive habitat model for the Tiger Spiketail developed by the NJDEP Endangered and Non-Game Species Program (ENSP) that employs a 500-meter buffer around all known records (NJDFW 2012a). This buffer distance was apparently somewhat arbitrarily selected by the ENSP biologists because “insufficient information exists in the scientific literature to support the designation of an occurrence area.” and “Due to the absence of literature concerning Odonate species’ spatial requirements, a 500-meter radius was formulated based upon the expert opinion of the biologist responsible for reviewing these species within the NJ Endangered and Nongame Species Program.” (NJDFW 2012b). In New York, an Element Distribution Model (EDM) for *C. erronea* was developed utilizing 44 potential habitat variables. The EDM identified the eight most important variables for potential habitat as topography, presence of water, slope, surficial geology, bedrock geologic class, percent shrub cover, percent wetland cover and May precipitation (Howard and Schlesinger 2012, NYNHP 2009b). The predictive nature of this model for finding new *C. erronea* sites is rated as fair (Howard

and Schlesinger 2012). The radio-telemetry data from the current study was compared to the NJDEP ENSP predictive model for one of the study streams to test its validity. Based on the plotting of the radio-telemetry locations for all six males, the 500-meter buffer may be an appropriate level of habitat protection as all of the data points fall within that buffer. (Kissling *et al.* (2014) note that radio-telemetry estimates of home range may under represent the actual extent due to limitations of short battery life and the impact from weight-induced behavioral changes Further study is likely warranted especially as even lighter radio-transmitters become available.

The radio-telemetry data from this study is the first obtained for *C. erronea* and despite potential limitations provides a deeper understanding of its life history than was previously available. As suggested by Wikelski *et al.* (2010), we agree the results of radio transmitter studies should be interpreted carefully (Wikelski *et al.* 2010). Although many insects are capable of carrying relatively heavy weight relative to their own body mass (Kissling *et al.* 2014), the potential behavioral impact of radio-transmitters upon individual insects carrying them has not been well-evaluated (Kissling *et al.* 2014). Radio telemetry studies have been conducted on crawling insects such as crickets (Kelly *et al.* 2008, Stringer and Chappell 2008, Sword *et al.* 2008, Watts and Thornburrow 2011, Watts *et al.* 2012) beetles (Dubois and Vignon 2008, Hedin *et al.* 2008, Negro *et al.* 2008, Rink and Sinsch 2007, Svensson *et al.* 2011) and the Giant Weta (Gibbs and McIntyre 1997, Stringer and Chappell 2008, Watts *et al.* 2012, Watts and Thornburrow 2011), or with insects that have strong flight capabilities, such as large beetles (Hedin and Ranius 2002, Sprecher-Uebersax and Durrer 2001), dragonflies (Wikelski *et al.* 2006), crickets (Fornoff *et al.* 2012), and bees (Hagen *et al.* 2011, Pasquet *et al.* 2008, Wikelski

et al. 2010). When reported, the ratio of transmitter mass to body mass of individual insects in these studies ranged from two to 100 percent but was most often less than one third of the body weight of the insect (Kissling *et al.* 2014). Although we cannot quantify the impact of the transmitters used in the present study, the rapid flight into the canopy upon release and the long range movements of individual dragonflies suggest that *C. erronea* is capable of carrying heavy loads. This is not necessarily unexpected given the ability of male dragonflies to carry females when in tandem and to carry large-size prey (Corbet 1999, Wakeling and Ellington 1997). Additionally, the longevity of the radio-tracked dragonflies strongly suggests they were able to feed with the transmitters attached. Dragonfly flight is energetically demanding (Baird and May 1997) and Polcyn (1994) found that high food inputs are necessary to sustain flight.

For dragonflies, a study by Wikelski, *et al.* (2006) demonstrated that *Anax junius* were capable of carrying a 300 mg radio transmitter with little apparent difficulty. Three of the darners in that study were weighed (mean $1.2\text{ g} \pm 0.3$ S.D.) indicating that transmitter weight was as much as 25 percent of body weight. A 0.22 mg radio transmitter was utilized on *M. quadratus*, *E. vitigera* and *Macromia cincta* (Jia and Wei 2012) that weighed approximately 1.0 g, a transmitter to body weight ratio of approximately 20 percent. The researchers reported that apparently normal flight behavior was observed although they were unable to assess the impact of the transmitter on behavior. A radio telemetry study on the Emperor dragonfly (*Anax imperator*) using transmitters weighing 0.29 g indicated the dragonflies could successfully defend territories and fly long distances (Levett and Walls 2011). *Anax imperator* weight has been reported to range from 1.2 to 1.5 g (Lotek undated) suggesting the transmitters in that study were about 19

to 24 percent of body weight. The weight of the transmitters used for the present study of *C. erronea* weighed 0.2 g. (M. May (unpublished data) reported a mean weight 0.560 g for 5 male *C. erronea* from New Jersey suggesting a transmitter to body weight ratio of approximately 36 percent in the current study. While this is higher than the other dragonfly telemetry studies, it is below other studies conducted on Coleoptera, Orthoptera, Hymenoptera and Megaloptera (Kissling *et al.* 2014). The utility of the *C. erronea* radio telemetry is also supported by unpublished mark-recapture data (Moskowitz and May, Chapter 5) that shows strong site fidelity and movement throughout the adjacent forest.

Conservation Recommendations

Based on the telemetry data and habitat characteristics, *C. erronea* is reliant upon large mature forests and high water quality streams. *C. erronea* is almost certainly highly sensitive to landscape changes that reduce forest cover adjacent to breeding streams and that alter stream hydrology and quality. These streams all share common characteristics including ground water seepage hydrology and extensive adjacent mature forest (Barlow 1995; Glotzhober 2006). Populations of the Tiger Spiketail in New Jersey (and likely throughout most of the northeast) have almost certainly declined from development and the conversion of forest to agriculture. A significant portion of the New Jersey range falls within some of the wealthiest counties in the country, creating residential development pressures (USCB 2015). The state is also facing many new above and below-ground utility lines and upgrades and other infrastructure pressures (NJDEP 2015). Many of these are located in the range of the Tiger Spiketail and at least potentially cross the habitat. The range of the Tiger Spiketail and its habitat also corresponds to mountaintop

mining and the extensive recent development of the Marcellus shale natural gas reserves and associated distribution pipelines, activities that may impact the high quality streams required by the species (Olcott 2011). *C. erronea* has also been ranked as having High Regional Vulnerability suggesting that a regional conservation strategy is necessary to insure its protection (White *et al.* 2014).

The limitations of the New Jersey and New York habitat models suggest a better understanding of the habitat could refine the predictive nature of the existing models, assist with locating any additional populations, and in developing appropriate conservation measures. Without better models, habitats are likely to be unidentified and impacted. Removal of forest cover has been shown to significantly alter stream hydrology (Hornbeck *et al.* 1970, Thorton *et al.* 2000). Small headwaters streams may also be more susceptible to increased temperature impacts than larger streams (Swift and Messer 1971). Forest clearing and riparian zone impacts can also affect aquatic insects, and the small headwaters streams utilized by *C. erronea* and other *Cordulegaster sp.* may be particularly sensitive (Gage *et al.* 2004). Gage *et al.* (2004) found substantially higher numbers of Cordulegastridae larvae in low impact headwaters streams in North Carolina than either irregularly impacted or highly impacted streams (Number of larvae collected within multiple 0.5 m² plots along 100 meter stream segments: Low Impact = 36, Irregularly Impacted = 25, Highly Impacted = 4).

It is evident that protection strategies for *C. erronea* need to focus on the maintenance of large contiguous forested areas adjacent to breeding streams and the protection of groundwater seepages and stream hydrology. The studies reveal a species that is heavily dependent on the canopy above the breeding stream and the adjacent forest. The

importance of expansive forest adjacent to breeding streams of forest dragonfly species is clear (Rivera 2006) and may be particularly important for Cordulegastridae. Walker (1958) noted that *Cordulegaster maculata* was generally observed foraging within a “hundred yards of the stream, but sometimes at a distance of nearly a mile.” Glotzhober (2006) observed two marked *C. erronea* moved 0.44 km and 0.58 km from their initial capture points. Müller (2000) reported *C. heros* 500 to 1,000 meters from the breeding stream. A protection strategy proposed for *Cordulegaster heros* in Hungary advocated the importance of “maintaining riparian forests in near pristine condition.” (Boda *et al.* 2015). This also seems appropriate for *C. erronea* as Barlow (2001) reported that a population of *C. erronea* in New Jersey was rapidly declining due to the removal of the surrounding forest canopy. Mark-resighting data (Moskowitz and May, Chapter 5) show movement of *C. erronea* between streams separated by approximately 500 meters of contiguous forest indicating that maintaining forested connectivity between breeding streams is likely critically important to insure interchange between breeding streams and genetic diversity. Based upon our studies, we recommend the following conservation elements:

- The protection of the entire watershed of the breeding stream.
- The protection of all contiguous forest between breeding streams.
- The addition of a 1,000 meter buffer around the entire watershed protection zone.
- Prohibiting forestry in the protected habitat.
- Prohibiting water extraction or other activities that will impact the breeding stream hydrology.

- Prohibiting activities that will impact water quality or temperature of the breeding stream.
- Development of more refined predictive models.
- Further studies across the range of the species.

Habitat conservation measures for *C. erronea* will also serve at least in part, to conserve other *Cordulegaster* species that are found in the same watersheds including *C. maculata* and *C. obliqua* (Barlow 2000, Glotzhofer 2006). In New Jersey, *C. erronea* habitats are also shared by the Mocha emerald and the Southern Pygmy clubtail. The later three species are all of conservation concern in the state (Bangma 2006). Other Odonate species of conservation concern may also occur in *C. erronea* watersheds including the Gray Petaltail (*Tachopteryx thoreyi* Hagen in Séllys) (NYNHP 2013) suggesting that protection of *C. erronea* habitats can result in the conservation of a suite of species. We hope this study will assist resource managers with the conservation of the Tiger Spiketail, a beautiful and charismatic dragonfly occurring in equally beautiful, cool, forested, spring and seepage fed streams.

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Chapter 4

Mate Recognition and Mating in the Tiger Spiketail Dragonfly (*Cordulegaster erronea* Hagen) (Odonata; Anisoptera)David Moskowitz¹ and Michael L. May²**Abstract**

Odonates are excellent subjects for mate recognition studies and many investigations have been conducted particularly for territorial species. For non-territorial species, such as the Cordulegastridae, mate recognition studies are complicated by the elusive and unpredictable nature of the females at the breeding streams. The releasing stimuli involved in recognition of potential mates by male Odonata have been investigated in several species, but basic information on mate recognition for the vast majority of Odonata is lacking. Among Cordulegastridae, although their distinctive oviposition behavior is well-known, only two short studies have specifically focused on mate recognition. In order to investigate how male Tiger Spiketail dragonflies (*Cordulegaster erronea* Hagen) recognize females, we presented patrolling males with a variety of dragonfly and model-based choices to simulate various characteristics of conspecific females. We also observed mating for the first time and numerous oviposition bouts, and recorded pertinent information about these events. We were able to identify several

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behavioral and physical attributes that evidently contribute to male recognition of females including movement, color and shape. These stimuli in order of importance are: vertical up and down movements, dark coloration, and the presence of wings on a dark, elongate object. We also discuss apparent mating strategies of the males and females. The Cordulegastridae retain many primitive characteristics and possess a broad suite of interesting behavioral attributes that may be useful for investigating the evolution of mating systems in Odonata.

Key Words: Odonata, dragonfly, *Cordulegaster erronea*, life history, oviposition, mating, mate recognition, New Jersey.

Introduction

The releasing stimuli involved in recognition of potential mates by male Odonata have been investigated in several species (Corbet 1999). In some species these are surprisingly non-specific (Gorb 1998, Paulson 1974, Robertson and Paterson 1982), but the suite of cues so far identified include body and/or wing color (Andrew 1966, Buccholz 1951, 1956; Jacobs 1955, Krieger and Krieger-Loibl, 1955), body shape (Mokrushov 1992, Pajunen 1964, Parr and Parr 1974, Ubukata 1983), and flight pattern (Miller and Miller 1985, Ubukata 1983), including oviposition movements (Jacobs 1955). In some species oviposition apparently inhibits male response (McMillan 2006, Miller and Miller 1985). Basic information on mate recognition for the vast majority of Odonata is lacking. Among Cordulegastridae, although their distinctive oviposition behavior has been

described repeatedly, only two short studies specifically focused on mate recognition are known to us (Ishizawa 2005, Ishizawa and Arai 2003) and none for the genus *Cordulegaster*.

Dragonflies of the genus *Cordulegaster sensu lato*, are large and boldly marked with black and yellow coloration. Females share a unique spike-like ovipositor. The genus is small consisting of 24 species and subspecies distributed across the Northern Hemisphere in both Eurasia and North America (Needham *et al.* 2000). Many species are geographically restricted, patchily distributed and often rare. The biology of most is also poorly understood (Glotzhofer 2006, Silsby 2001). *Cordulegaster* habitats are typically small to medium-sized woodland or meadow streams with sand or silt bottoms (Corbet 1999, Needham *et al.* 2000, Paulson 2012). *Cordulegaster* males patrol these linear habitats coursing up and down the streams, often for long periods, (Kaiser 1982, Alcock 1985) and are easily observed. Male *C. erronea* behave similarly but patrolling is typically infrequent and of short duration (Barlow 1995, Glotzhofer 2006). Numerous males often patrol the same streams at the same time. Interactions between patrolling males, even at high densities, are infrequent, brief, and of low intensity. Females appear at the streams much less frequently and throughout the day. Females oviposit unguarded, hovering in a nearly vertical position repeatedly thrusting the ovipositor into the substrate, accompanied by up-and-down movement of the whole body (“bobbing”). Oviposition bouts may continue for as long as ten minutes within a small area. Prior to our study, mating by *C. erronea* had not been reported.

The particular focus of this study was to investigate cues by which male *C. erronea* recognize potential mates and to explore mating behavior in the species. We presented patrolling males with a variety of natural dragonflies and models that, to varying degrees and in varying combinations, provided visual stimuli that appeared to simulate characteristics of conspecific females. We also observed mating and recorded pertinent information about each event. In this way we were able to identify several features that evidently contribute to male recognition of females as potential mates. We also discuss possible mating strategies of both sexes.

Study Location

The study was conducted at two *C. erronea* breeding streams on the Schiff Reservation Natural Lands Trust in Mendham Township, Morris County, New Jersey (40.764470, -74.620918). The streams are located at the bottom of broad forested valleys in the Highlands Physiographic Province of New Jersey. The Highlands Physiographic Province is characterized by a series of flat-topped ridges composed of crystalline, igneous, and metamorphic rocks separated by deep narrow valleys underlain by less resistant limestone and shale (Robichaud and Buell 1973).

Both streams are perennial headwaters fed by numerous groundwater seepages and are separated by a forested topographic divide of about 500 meters. The more easterly stream is approximately 1,200 meters in length and is approximately 1-3 meters wide with a gravelly and silty bottom. The second, more westerly stream is approximately 600 meters long. Most of the stream has a well-defined channel ranging in width from about 1-3

meters. There is also a broad rocky area with a poorly-defined channel that is approximately 5 meters wide. Water depths in the streams rarely exceed 0.3 meters and flow is nearly imperceptible. Even during a prolonged drought, there was at least partial flow in the study streams. Both streams flow through mature, mixed-deciduous forest. Undercut banks and overhanging vegetation characterize the streams and skunk cabbage (*Symplocarpus foetidus* (L.) Salisb. ex W.P.C. Barton) is scattered within and along the channels and in the many seepages that feed them. The stream bottoms are interspersed sandy, gravelly and silty areas. The streams are consistent with other breeding streams for *C. erronea* in New Jersey (Barlow 1995, pers. obs. Moskowitz, NJDFW, 2012), Ohio (Glotzhober 2006), New York (NYNHP 2012) and elsewhere in the range (Needham *et al.* 2000, pers. obs. Moskowitz).

Methods and Materials

A variety of stimuli were utilized to investigate potential female cues for male recognition of receptive females. These included various presentations of living and dead male *C. erronea*, dead male Slaty skimmer (*Libellula incesta* Hagen) and artificial models. For the *C. erronea* trials, only males were utilized due to the infrequency of females at the breeding streams, the overall rarity of the species and the desire to minimize impacts to females. *L. incesta* was selected as a surrogate for *C. erronea* because of its dark coloration, availability, abundance and relative size. For the trials, both *C. erronea* and *L. incesta* were presented as natural specimens and as specimens painted white (only *L. incesta*). Models were constructed from wooden dowels (0.7 cm diameter and 7.6 cm in length) painted in various colors and with or without wings (Figure 1). Wings were obtained from *L. incesta* and were glued to the dowel in a manner

approximating natural wings. In all experiments the dragonfly or model was tethered vertically to a 122 cm to 152.4 cm length of black sewing thread that was suspended from a pole similar to Moore (1952). The tethered dragonflies were bobbed with an up and down motion approximating the movements of an ovipositing female. Each insect or model was presented to patrolling males for 25 or more repetitions (Range = 26-28) while hanging as motionless as possible and for at least an additional 25 repetitions (Range = 25-41) while being bobbed up and down simulating the movements of an ovipositing female *C. erronea*. Although multiple males were present on the streams during the various trials, most were not individually marked, so multiple presentations to the same male inevitably occurred. However, to minimize this potential, the studies were conducted over multiple days and on both streams. Unpublished data (Moskowitz and May 2015) with marked males also suggests that individual males are only present on the breeding streams for short periods each day, further minimizing the potential for the same individual dragonfly to be exposed repeatedly to the same test. As suggested by P. Morin (pers. communication), the presentations of the models and insects were also varied to lessen the potential for repeated exposure by the same individual to the same test. Various presentations were compared utilizing Fishers Exact Test (Fisher 1954) to determine the significance of color, shape and movement.

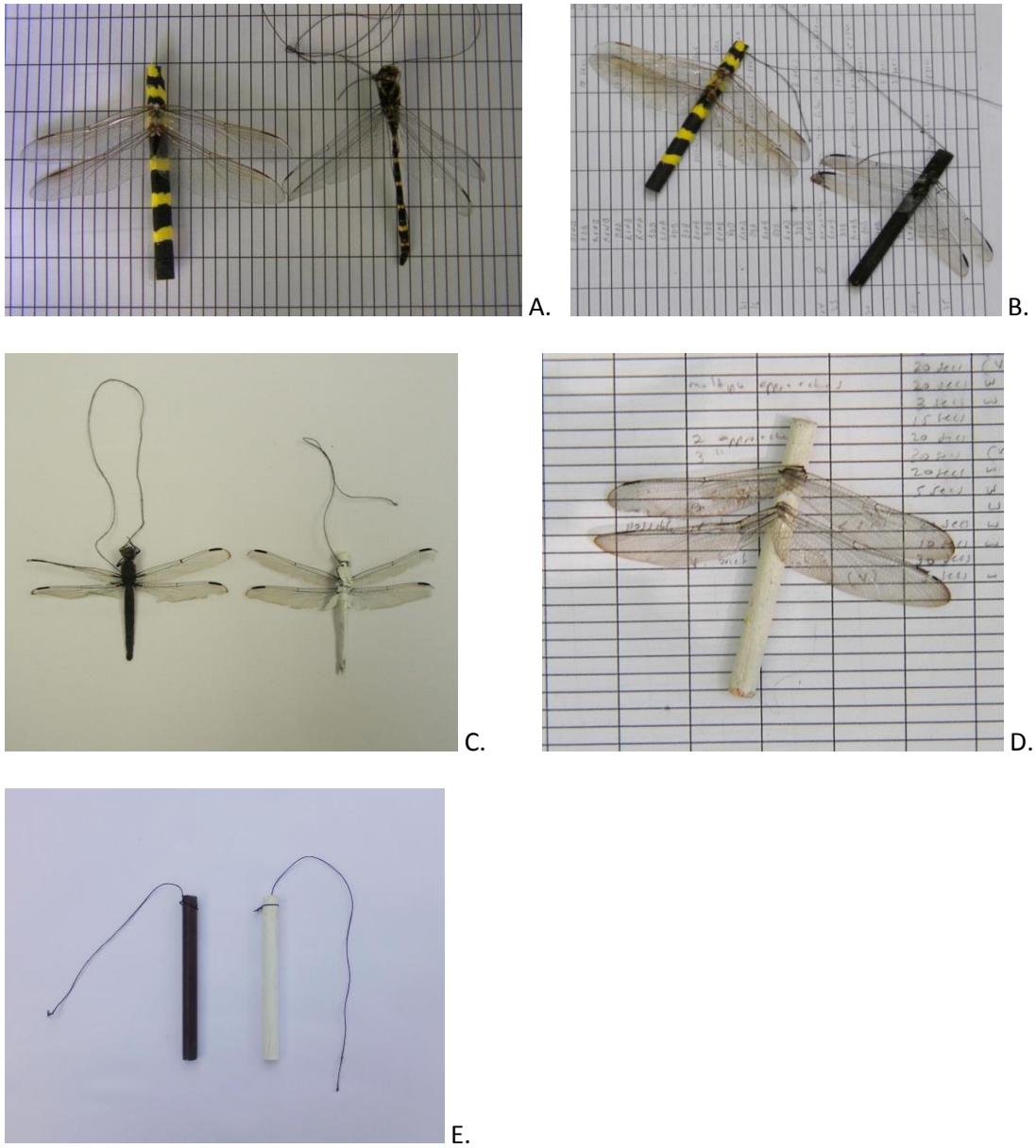


Figure 1. *Cordulegaster erronea* study presentations. (A). *C. erronea* model and male *C. erronea*. (B). *C. erronea* model and black dowel model. (C). Male *Libellula incesta*, natural and painted white. (D). *C. erronea* white dowel model. (E). Black and white dowel models.

Additional similar, but less intensive trials, were also conducted on Twin-spotted Spiketails (*Cordulegaster maculata* Selys) (N = 5) and Arrowhead Spiketails (*Cordulegaster obliqua* Say) (N = 25) in New Jersey and Delta-spotted Spiketails (*Cordulegaster diastatops* Selys) in Pennsylvania. For *C. obliqua* and *C. maculata*, presentations to patrolling males were limited to a bobbed model, painted with black and yellow stripes and with the wings of *L. incesa*. For *C. diastatops*, presentations to patrolling males included a bobbed black dowel with no wings (N = 25) and stationary (N = 25), a live tethered *C. diastatops*, bobbed (N = 25) and stationary (N = 25) and a bobbed (N = 9) and stationary (N = 5) white dowel with no wings. Very limited observations were also made with a small battery operated rotating fan placed on a rock just slightly above the water surface and near the center of the stream in the manner of Ishizawa (2005) and Ishizawa and Arai (2003). The fan was run on one day for approximately 3.25 hours. The fan was presented in three positions: facing downstream with the blades vertical; toward the stream bank with the blades vertical; and with the blades horizontal and pointing upward. Systematic trials were not conducted but interactions with the fan were recorded when observed.

In an effort to determine how much time a female had to oviposit before a male appeared at that location we also recorded the amount of time before and after she began ovipositing that a male flew by the oviposition site. The time before and after a male passed by an oviposition site was recorded for 51 males before the ovipositing began and for 41 males after the ovipositing ended.

Results

In our study, female stimuli appear to be the sensory cues for patrolling males to locate and recognize females. These stimuli in order of importance are: vertical up and down movements, dark coloration, and the presence of wings on a dark, elongate object. Table 1 provides the results of each trial. Of the 14 various presentations, only four resulted in the male making contact with the tethered insect or model more than five percent of the time and all were with a bobbed, dark insect or model with wings: *L. incesta* (34/41 = 83%), *C. erronea* (19/32 = 58%), black dowel model (12/25 = 48%) and *C. erronea* model (12/31 = 39%). When any response by the male was observed, only seven of the 14 presentations elicited a response more than 40 percent of the time and all featured tethered insects or models that were dark and bobbed: *L. incesta* (40/41 = 98%), black dowel model with wings (23/25 = 92%), *C. erronea* (28/32 = 88%), *C. erronea* model (24/31 = 77 %), *C. erronea* without wings (18/25 = 72%), *C. erronea* model without wings (16/25 = 64%) and black dowel without wings (16/25 = 64%). These results provide strong evidence that a combination of vertical up and down movement and dark coloration are the cues for males to recognize a female and to attempt mating. The presence of wings also appears to be important but less so than movement and dark coloration, at least for initial recognition.

The presentations were also compared to test the relationship between bobbing and stationary insects and models, dark and light insects and models, and the presence of wings or no wings. Table 2 summarizes the probabilities of differences between responses to specific pairs of models. Bobbing and dark coloration are highly significant for eliciting a male response ($p < .05$).

Table 1. Male *C. erronea* response to various presentations

#	Presentation	# Obs.	No Response	Brief Pause	Face Off	Clasping	Mating Attempt	Tandem Flight	Proportion Response		Proportion Response	
1	<i>C. erronea</i> (intact, bobbed)	32	3	0	22	19	14	8	28\32	88%	19/32	58%
2	<i>C. erronea</i> (intact, not bobbed)	28	28	0	0	0	0	0	0\28	0.0%	0/28	0.0%
3	<i>C. erronea</i> (no wings, bobbed)	25	7	5	13	1	0	0	18\25	72%	1/25	4.0%
4	<i>C. erronea</i> (bobbed, painted white)	25	0	10	0	0	0	0	10\25	40%	0/25	0.0%
5	<i>C. erronea</i> model (intact, bobbed)	31	3	2	24	12	10	0	24\31	77%	12/31	39%
6	<i>C. erronea</i> model (intact, not bobbed)	26	22	0	0	0	0	0	0\26	0.0%	0/26	0.0%
7	<i>C. erronea</i> model (no wings, bobbed)	25	2	5	11	0	0	0	16\25	64%	0/25	0.0%
8	<i>L. incesta</i> (intact, bobbed)	41	1	1	37	34	26	1	40\41	98%	34/41	83%
9	<i>L. incesta</i> (intact, not bobbed)	26	21	0	0	0	0	0	0\26	0.0%	0/26	0.0%
10	<i>L. incesta</i> (intact, white bobbed)	25	7	1	3	1	0	0	5\25	20%	1/25	4.0%
11	Black dowel model (bobbed)	25	2	0	23	12	9	0	23\25	92%	12/25	48%
12	Black dowel (no wings, bobbed)	25	8	3	13	0	0	0	16\25	64%	0/25	0.0%
13	White dowel (bobbed)	25	19	5	1	0	0	0	6\25	24%	0/25	0.0%
14	White dowel (no wings, bobbed)	25	0	6	0	0	0	0	6\25	24%	0/25	0.0%

This combination, when further combined with wings and natural insects (as opposed to models), also elicits a strong male response that was highly significant ($p < .05$), especially when comparing whether males made contact. Vertical movement and dark coloration without wings was also strongly correlated with a male response to the presented trial. Deviations from these stimuli such as a lack of movement, light coloration and light coloration without wings were highly significant ($p < .05$) for a lack of a response by male *C. erronea*.

A small battery operated fan was presented to patrolling male *C. erronea* to investigate if it would elicit a response as reported by Ishizawa (2005) and Ishizawa and Arai (2003) for the Golden Ringed dragonfly (*Anotogaster sieboldii* Selys) and the rotated “dummy” presented to the Common Clubtail (*Ictinogomphus pertinax* Hagen in Selys) and the Marsh Skimmer (*Orethetrum luzonicum* Brauer) by Kano (2007). Observed responses by the patrolling males were limited to the fan facing downstream with vertical blades and included; hovering in front of the fan for 10 to 15 seconds, slowing but continuing to patrol, and possibly turning back and continuing in the other direction.

The limited field trials on the Twin-spotted Spiketail (*Cordulegaster maculata* Selys) and Arrowhead Spiketail (*Cordulegaster obliqua* Say) in New Jersey and the Delta-spotted Spiketail (*Cordulegaster diastatops* Selys) in Pennsylvania, yielded different results from those observed for *C. erronea*. Nonetheless, they also suggest that the dark color and oviposition posture and movement of the female may play some role in male recognition of females, at least in some other *Cordulegaster* species. For example, *C. maculata* showed no interest in a bobbed model presented five times. The same model was presented to *C. obliqua* and the males either showed

Table 2. Results of Fisher Exact Test for male *C. erronea* response to compared presentation pairs.

Presentation*	Any Response		Contact	
	p-value	Odds Ratio	p-value	Odds Ratio
1 v 2	<i>3.55x10⁻³</i>	**	--	--
1 v 3	0.184	2.673	<i>1.20x10⁻⁵</i>	32.96
1 v 4	<i>2.20x10⁻⁴</i>	9.989	--	--
1 v 5	0.337	2.018	0.133	2.282
1 v 7	0.0558	3.839	--	--
1 v 8	0.165	0.179	<i>0.0348</i>	0.306
1 v 11	0.686	0.613	0.432	1.570
1 v 13	<i>1.56x10⁻⁶</i>	20.48	--	--
1 v 15	0.372	0.297	<i>1.20x10⁻⁵</i>	32.96
5 v 3	0.759	1.326	<i>3.16x10⁻³</i>	14.55
8 v 10	<i>2.46x10⁻¹¹</i>	138.00	<i>8.84x10⁻¹¹</i>	104.19
12 v 14	<i>9.59x10⁻³</i>	5.416	--	--
11 v 13	<i>1.62x10⁻⁶</i>	32.89	--	--

*Refer to Table 1 for presentation type. **Odds ratio cannot be computed because denominator is zero. Cells with "--" indicate no comparison was made owing to absence of contact with one model. Significant differences in bold italics.

no interest ($15/25 = 60\%$) or briefly paused ($10/25 = 40\%$) but never had contact with the model. *C. diastatops* showed a strong reaction ($23/25 = 92\%$) to a bobbed live male *C. diastatops* including three attempts at clasping ($3/25 = 12\%$); to a bobbed model with wings ($17/27 = 63\%$); interest in, but no contact with a bobbed black dowel with no wings ($11/25 = 44\%$); almost no interest in a live *C. diastatops* male that was stationary ($2/25 = 8\%$); a stationary black dowel with no wings ($0/25 = 0\%$); a stationary ($0/5 = 0\%$) and a bobbed ($1/9 = 11\%$) white dowel with no wings, and a yellow and black stationary model with wings ($0/7 = 0\%$).

During our study, female *C. erronea* were observed 63 times with six mating attempts and two other possible attempts. The earliest a female was observed at the streams was 9:58 am and the latest at 7:44 pm (Figure 2). Sixty of these observations involved ovipositing ranging from the first at 9:59 am to the last at 7:44 pm when the stream and oviposition site were very dark. The other three females were flying along the stream. Females were occasionally observed thrusting the end of the abdomen into the sediments from a few, to as many as 15 times, at a number of locations, before settling in to an often lengthy ovipositing bout. These shorter bouts may have been exploratory thrusts testing the suitability of the location. On four occasions, the length of time the female oviposited and the number of thrusts into the sediments was recorded from start to finish. These included in order of length: 5 minutes with 221 thrusts; 6 minutes with 217 thrusts, 10 minutes with 914 thrusts, and 12 minutes with 842 thrusts (Mean ovipositing time = 8.3 minutes \pm 3.3), (Mean number of thrusts = 549 thrusts \pm 382) and (Mean number of thrusts per minute = 60.5 \pm 25).

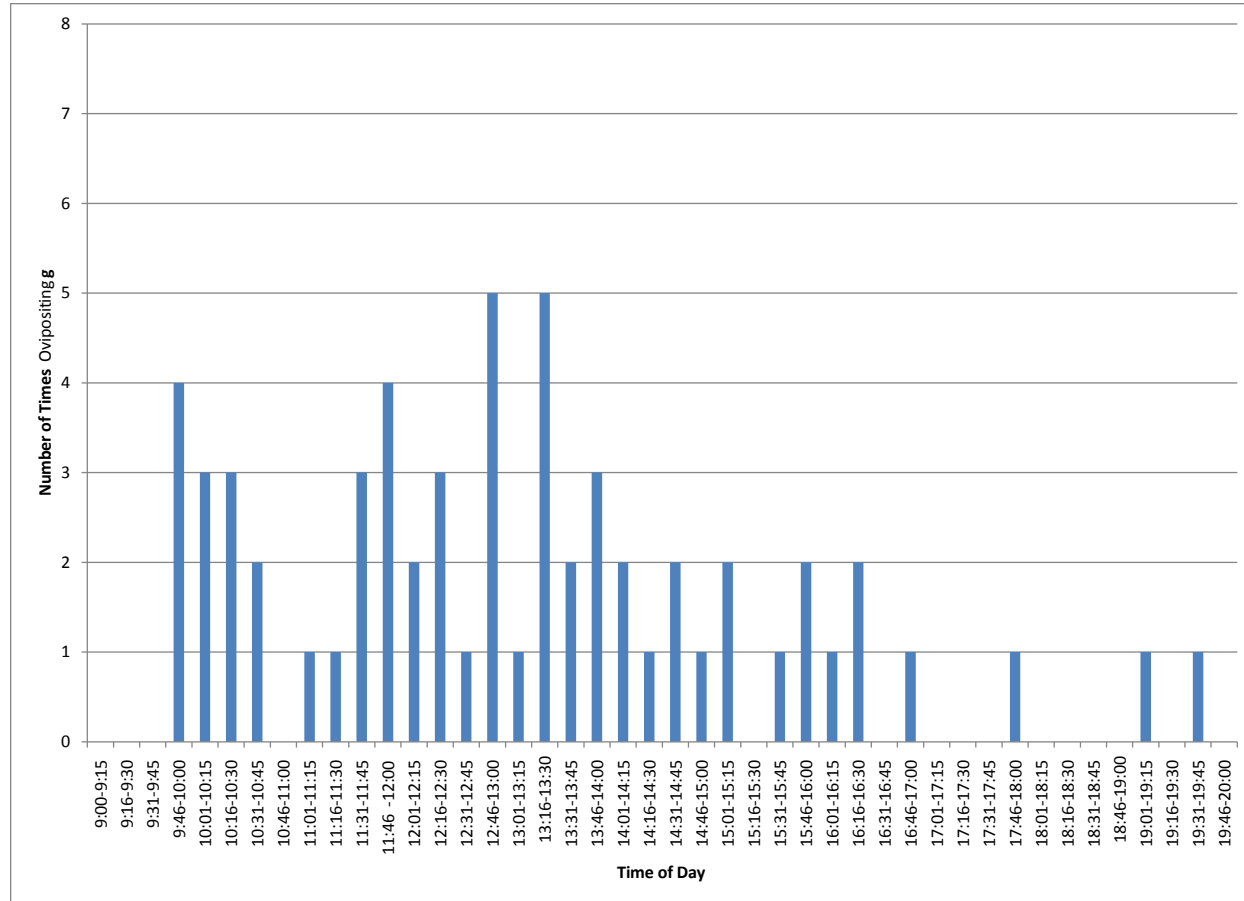


Figure 2. Hourly distribution of ovipositing by *C. erronea*.

Confirmed pre-mating was observed six times. Each time, the male rapidly approached the female, clasping her and the pair then rapidly flew in tandem away from the stream. Five of the pairs flew directly upward into the canopy. One pair perched briefly on a branch about 6 meters high before continuing to the canopy. One of the pairs also appeared to briefly enter the mating wheel while in flight before decoupling and continuing into the canopy in tandem. In five of these mating observations, the female was initially ovipositing and on the other she was flying low over the water when a male grabbed her. On one occasion, an ovipositing female was grabbed by a male and an intense interaction ensued for about 10 seconds. After the first few seconds in the air just a few centimeters above the water, the pair tumbled into the stream and the contact continued for a few more seconds with both dragonflies in the water. The male then released the female and flew off the stream and into the canopy. The female remained motionless for a few more seconds before also flying off the stream and into the canopy. During the remainder of the observed ovipositing bouts the females were not harassed by a male. Females also frequently oviposited behind objects such as logs and rocks or beneath overhanging vegetation in ways that appeared to obscure their visibility to patrolling males. Of the 48 females with detailed oviposition site information, twenty-seven (56 %) oviposited in an obscured location beneath or near skunk cabbage, a sedge, rocks, logs or the overhanging stream banks (Table 3).

Females also often oviposited at times when males were not at the oviposition site. The mean time for a male to pass by the location where a female would oviposit was 12 minutes \pm 15 (Range = 1 - 60 minutes) and the mean time following oviposition was 13 minutes \pm 18 (Range 1 – 85 minutes).

Discussion

Odonates are excellent subjects for mate recognition studies and many investigations have been conducted particularly for territorial species (Corbet 1999). For non-territorial species, such as the Cordulegastridae (Alcock 1985, Kaiser 1982) mate recognition studies are complicated by the difficulty of observing mating and the often elusive and unpredictable nature of the females appearing at the breeding streams (Fincke, *et al.* 1997, Glotzhober 2006, Kennedy 1917). Nonetheless, *C. erronea* seems well-suited for mate recognition studies for a number of reasons: the males are easily observed as they patrol along the breeding stream actively searching for females; *C. erronea* is often the only dragonfly regularly observed at the breeding streams, eliminating potential interference from other species, and the females have a distinctive ovipositing posture that is often of long duration and therefore easily observed. The Cordulegastridae also retain many primitive characteristics and therefore may help shed light on the evolution of mating systems in Odonata (Carle *et al.* 2015, Fraser 1929, Fraser 1933, Hančíková 2014, Kaiser 1982, Ware *et al.* 2007, Ware *et al.* 2008).

Our study suggests that recognition of females and the response by males is evidently stimulated mainly by visual cues related to the movement and color of ovipositing females. In combination these cues apparently provide strong stimuli for a patrolling male *C. erronea* to locate, recognize, grab, clasp and mate with an ovipositing female.

Table 3. Characteristics of ovipositing *C. erronea* females.

# Females	Male Present	Ovipositing	Flying	Obscured Site	M/F Interaction	M/F Contact
63	13 (21.0%)	60 (95.24%)	3 (4.76%)	27 (42.86%)	9 (14.25%)	6 (9.52%)

One female was taken in flight by a patrolling male and it is unclear how she was recognized but we may have only observed part of the interaction. Movement by the female in other odonate species has been shown to be important for male recognition (Andrew 1966, Bick and Bick 1961). Ubukata (1983) observed that patrolling male Downy Emeralds (*Cordulia aenea amurensis* Selys) were generally unable to detect a motionless female. In the only instance we observed of *C. erronea* showing interest in any other insect on the streams, a male was observed briefly investigating an ovipositing crane fly (Tipulidae, Diptera). The crane fly was moving in an up and down motion similar to the movements of an ovipositing Tiger Spiketail. Interestingly, Kennedy (1915, 1917) also remarked how similar the ovipositing movement of *C. dorsalis* is to a crane fly. The only time we observed *C. erronea* interacting with another dragonfly was when a male *S. tenebrosa* appeared to chase a patrolling male off the stream.

Our observations also suggest that copulation by *C. erronea* is almost certainly in the canopy. Although not quantified, males that made contact with the tethered insect or a model often attempted to fly upwards toward the canopy with the model in tandem. Ovipositing females always flew rapidly up into the canopy upon completion. The six times a male grabbed a female and flew in tandem, the flight was also always up toward the canopy. In one instance, the pair could be visually followed as it flew upward through the trees to the top of the canopy and then downstream.

C. erronea females were often observed ovipositing behind objects such as logs and rocks or beneath overhanging vegetation in ways that appear to obscure their visibility to patrolling males. Presumably the females are ovipositing in these locations to reduce the potential for harassment by males. Ubukata (1984) found that *Cordulia aenea amurensis*

females oviposited in vegetation that helped hide them and make an approach by a patrolling male difficult. Hilton (1983) noted a similar situation with American Emerald (*Cordulia shurtleffii* Scudder) where the females typically oviposit hidden by vegetation.

Male *C. erronea* patrol along the stream methodically searching beneath and near overhangs, vegetation, large rocks and fallen logs. Based on our study results and field observations, searching males that encounter the female cues of dark coloration and vertical movements are often rapidly stimulated into mating actions. However, on eight occasions, a patrolling male flew in close proximity to an ovipositing female without exhibiting any obvious interest although she may not have been observed. Ubukata (1984) observed that previously mated *C. aenea* oviposited cryptically lessening the likely exposure to patrolling males. Hilton (1983) observed similar cryptic ovipositing behavior in *Cordulia shurtleffii* (Scudder). Could the *C. erronea* females observed ovipositing in hidden or obscured locations be behaving similarly? This could explain the seemingly methodical search method of *C. erronea* males while patrolling. Miller (1982) observed that intermittent hovering by patrolling male Black-tailed Skimmer (*Nesiothemis farinose* Förster) improved the ability to locate oviposting females in shaded places. Do *C. erronea* females only mate a limited number of times as reported for *C. diadema* (Alcock 1985) and these eight observations reflect some unnoticed behavioral aspects that alerted the male that the female is not receptive? Our observations indicate that *C. erronea* can oviposit without male interference for remarkably long periods of time and with hundreds of thrusts. Other *Cordulegaster* species are similar. Corbet (1999) reported more than 200 thrusts by *C. boltonii* and Kaiser (1982) noted a female ovipositing for more than 15 minutes. Walker (1958) reported 100 thrusts in one

minute for *C. maculata*. Drable (1905) reported 700-750 thrusts of about 70 to 75 per minute for a ten minute period of ovipositing by *C. annulatus* (sic *C. boltonii*). Stevenson *et al.* (2009) reported 70 thrusts at a rate of more than one per second for *C. sayi*. Our observations are similar for *C. erronea*. The majority of ovipositing females we observed were unmolested by males and often at the stream when no males were immediately present even when patrolling. This suggests a few possibilities: male densities are low enough that large stream segments are not patrolled at a given time; the females are selecting times and locations of less male activity; and/or they are providing an avoidance signal that they are not receptive.

Multiple male *C. erronea* commonly patrol the same stream segment at the same time, often in close proximity to each other. Interactions between males are infrequent, generally of short duration and rarely involve contact. They occur most often when males are patrolling toward each other. As the males approach, they pause for a few seconds face to face, and in close proximity to each other, before a brief chase of a few seconds upwards from the stream. These chases were rarely observed to reach a height of more than about 5 meters above the stream. After the chases end, both males typically return to the stream to continue patrolling, often in opposite directions. Similar observations have been made for *C. erronea* in Ohio Glotzhober (1986) and other *Cordulegaster* species including *C. diadema* Selys in Arizona (Alcock 1985) and *Cordulegaster boltonii* in Germany (Kaiser 1982).

Since *C. erronea* is typically the only odonate on the breeding streams, it is unlikely that male fighting is related to potential confusion over the species. It also seems unlikely that these interactions result from confusion over the sex of the individuals. Although *C.*

erronea males have a similar color pattern as females, patrolling males fly in a manner that is not in any way similar to the posture of an ovipositing female and her apparent sexual recognition signals of up and down vertical movement. Given the short duration of male aggressive bouts, and their apparent non-territoriality, it also seems unlikely that they relate to the “wars of attrition” observed by Marden and Waage (1990) in Ebony Jewelwing (*Calopteryx maculata* Beauvois). Kaiser (1982) suggested that fighting by patrolling males of the non-territorial *Cordulegaster boltonii* results in spacing between individuals that may lessen competition for the females that arrive at unpredictable locations along the stream. Although not quantified in our study, patrolling males were often observed following one another in close proximity, separated by less than a meter. Miller and Miller (1985) offer another possible explanation for male fighting in a non-territorial dragonfly. They suggest, that male interactions in the Small Pincertail (*Onychogomphus forcipatus unguiculatus* L.) relate to heightened male sexual readiness by maintaining a state of high arousal. Both theories seem plausible to explain the occasional, but brief aggression by male *C. erronea*, as multiple males often patrol at the same time, and same location, and the females appear unpredictably throughout the day, and along the entire stream. Spacing and readiness seem useful in this situation. While further study is needed on *C. erronea* and other Cordulegastridae, the family is basal to the higher Libelluloidea (Carle *et al.* 2015, Fraser 1929, Fraser 1933, Ware *et al.* 2007, Ware *et al.* 2008) and their behavior could help shed light on the evolution of mating systems in Odonata (Fincke *et al.* 1997, Hančíková 2014, Kaiser 1982).

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